Exploring the effects of habitat fragmentation on biodiversity

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

The work in Chapter 2 of the thesis has appeared in publication as follows:

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I was responsible for the initial idea, and then found and adapted the method, conducted the analysis and I lead the writing of the manuscript.

J.B. ad W.K. suggested I look for a more sophisticated methods than the one I initially proposed, consulted on my modifications to the method, presentation of the results and contributed critically to the drafts of the paper.

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Abstract

Debate rages as to whether, once habitat loss effects are discounted, habitat fragmentation leads to biodiversity declines or has positive effects. Studies define fragmentation in different ways, as the converse of connectivity, isolation of patches, or with habitat loss. Studies need to address “fragmentation per se”, which is, specifically, at the landscape level and not confounded by habitat loss. Different patterns have been found, suggesting that fragmentation per se does not always have a negative effect. To help bring clarity to the debate, I investigated some of the reasons for these differing results.

To investigate fragmentation per se, I developed a multi-species landscape-scale *individual-based model* (IBM), with species able to move around my simulated landscapes. I investigated species-level perspectives and incorporated the concepts from this analysis into IBM. I investigated, using the IBM, the effect of fragmentation per se of a focal-habitat on diversity across landscapes and if the effect differed with different species’ characteristics and modification of the land covers between patches of the focal-habitat.

I found species each have a unique unshared perspective of the multiple land covers in landscapes. It is inappropriate to lump species into being associated with one land cover. Overall gamma-diversity increases with fragmentation per se under a range of assumptions but species that are less competitive and prefer the focal-habitat decline. Specialists, generalists and species able to traverse the matrix to reach patches are unaffected or increase with fragmentation per se. Landscapes used in fragmentation studies are important in determining what result is found, with often-used landscapes tending to lead to more negative results.

These findings help resolve the fragmentation per se debate. While our study suggests general patterns of gamma-diversity increase under fragmentation, critically for conservation and policy responses, species associated with the fragmented habitat decline. But declines are not universal. Species are affected differently.

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Abbreviations

SDMs - Species distribution models

IndVal - Indicator Value Index of Dufrêne and Legendre (1997)

NBN - UK National Biodiversity Network

CEH – NERC Centre for Ecology and Hydrology, now UK Centre for Ecology and Hydrology

LCM2015 - Land Cover Map 2015

FPS - Fragmentation per se

IBM - Individual-based model

ODD - **O**verview, **D**esign concepts, and **D**etails protocol

RW - Random walk

CRW - Correlated random walk

HDW - Habitat dependent walk

Chapter 1

Introduction

Humans have modified much of the land surface of the world, converting habitats into other habitats and land uses for our own purpose (Lawton et al., 2010; IPBES, 2018). Doing so directly reduces the area of habitats and leaves what remains fragmented, with patches of habitat separated from each other by other land covers. The effect that habitat loss has on species diversity is clear, leading to a reduction in species (MacArthur and Wilson, 1967; Fahrig, 2003; Hodgson, Moilanen, et al., 2011; Keil et al., 2015; Loke et al., 2019). It had been shown that fragmentation also contributes to this loss in species diversity because it leads to a reduction in the ability of species to move between remaining patches of habitat (Haddad et al., 2015). But the consistent negative effect of fragmentation without habitat loss, *fragmentation per se* (FPS), is in debate (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019). Evidence has been presented that suggests that FPS may either have no effect or even potentially a positive effect on species richness (Fahrig, 2017; Rybicki et al., 2019). In this thesis I will theoretically explore some circumstances that could lead to FPS not having a negative effect on species diversity and help reconcile the two opposing sides in the FPS debate.

In this chapter, I first present the habitat fragmentation debate and issues surrounding how fragmentation is defined. I go on to talk about differences in scale of analysis and how these scales are defined. Then on how habitat is defined, including how species relate to habitat and how species move through landscapes. I then go on to explain the *individual-based modelling* (IBM) approach I will employ, and finally present my research questions and the structure of the rest of this thesis.

1.1 Habitat fragmentation - a contested concept

There are two widely accepted paradigms in biodiversity that come into conflict, that connectivity between habitat patches should be increased as connected patches have more species (Prugh et al., 2008; Haddad et al., 2015; Damschen et al., 2019) and that heterogeneous landscapes can support more species (Benton et al., 2003; Oliver et al., 2010). Increased connectivity allows for patches to be recharged by the immigration of individuals (Lawson et al., 2012) or for recolonization (Rosenzweig, 2002) and allows for gene flow between populations (Hooftman et al., 2016). Also in a world with a changing climate, increased connectivity will, it is hoped, allow for species movement to areas that become climatically suitable and escape areas that may no longer be suitable (Hodgson, Thomas, et al., 2011). There are potential issues with increasing connectivity, however. Increasing connectivity by adding more habitat patches could cause landscapes to become more homogenous and potentially fragment other habitats. Increased connectivity could lead to species homogenisation through the most competitive species spreading, potentially to the detriment of less widespread species. Increased connectivity can also facilitate the movement of predators, invasive species and disease and, particularly in the case of corridors, disturbance, for example, through the spread of fire (Haddad et al., 2014). Although the review conducted by Haddad et al. (2014) specifically looking at the negative effects of corridors, failed to find a consistent effect of corridors on predators, invasive species, disease, or disturbance, they did point out that the literature was deficient and that there is a need for studies looking at natural corridors at a larger scale than experimental systems. They also pointed out that despite corridors being "the most direct way to restore connectivity in conservation" that "[w]ith one exception (edge effects), [they] would expect the mechanisms by which corridors exert negative effects to be identical to those exerted by connectivity more broadly." (Haddad et al., 2014). Therefore, this work on corridors is relevant to work on connectivity and fragmentation more broadly.

Researchers often conflate connectivity with the inverse of fragmentation, assuming that higher fragmentation automatically leads to lower connectivity. But this may not be the case (Fahrig, 2017). Thompson et al. (2019) showed higher diversity in their modelling study, with their measure of effective connectivity when the landscape was more fragmented because their measure includes distance travelled and FPS, through increasing the number of patches, makes the new patches closer together than the original patches were. Fragmentation leads to reduced structural connectivity, but not necessarily functional connectivity, as this is a species-specific concept. One measure of functional connectivity is unlikely to be applicable to all species (Bélisle, 2005; Betts et al., 2014). Related to the assumption that fragmentation equals reduced functional connectivity, studies often represent fragmentation by increasing the distance between and isolation of patches (Haddad et al., 2017; Brodie and Newmark, 2019). However, this may not necessarily be the case. If the area of habitat is not reduced, and fragmentation leads to the number of patches being increased, then patches may end up being closer together (Fahrig, 2017). Because fragmentation generally is caused by the removal of habitat, studies of fragmentation often include habitat loss. Habitat loss has a large and consistently negative effect of biodiversity, and it has been shown that the effect of loss of area swamps the fragmentation component of studies (Fahrig, 2003; Fahrig, 2017; Fahrig, 2019; Fahrig et al., 2019). A solution to this frequent conflation and compounding was to define a new term, FPS (fragmentation per se). FPS is fragmentation in the absence of habitat loss (Fahrig, 2017). This form of fragmentation may be unrealistic as fragmentation in the real world is usually caused by habitat conversion and therefore a loss of area (Fletcher et al., 2018). But controlling for area does allow for isolation of the effects of fragmentation independent of the effect of habitat loss. FPS is a purely mechanical splitting of habitat, excluding any qualitative implications for functional connectivity, which is a species-specific concept. When considering landscape-scale fragmentation studies controlling for area loss, Fahrig (2017) found studies that found either no effect of fragmentation or a positive effect on species richness as well as other measures of the fitness of species and communities. Many fragmentation studies are a mix of single species analysis (Masier and Bonte, 2019; Galán-Acedo et al., 2019; Kimmig et al., 2019; Hauser et al., 2019; Marrotte et al., 2020), multi-species analysis, often of birds (Valente and Betts, 2019) or plant species (Damschen et al., 2019; Wilson et al., 2020) and meta-analysis (Watling et al., 2020; Kling et al., 2020). Many of the single species studies have looked at gene flow (Kimmig et al., 2019; Marrotte et al., 2020), used microcosm setups (Masier and Bonte, 2019), or looked at abundance (Galán-Acedo et al., 2019) and it is positive or negative responses of these sorts of studies that are often reported as positive or negative effects of fragmentation in meta-analysis studies along with general responses of species richness (Fahrig, 2017). Being unclear about which of these different measures of the effect of fragmentation are being talked about can be confusing and lead to the mistaken belief that positive and negative effects of FPS are on species richness (Miller-Rushing et al., 2019).

Species richness is the number of species and is analogous of alpha- and gamma-diversity at different spatial scales (Whittaker, 1972). Alpha-, beta- and gamma-diversity are different ways of quantifying biodiversity at and between defined scales (Socolar et al., 2016). As with all research, the scale is important to define in studies. A patch can be defined at multiple scales from a quadrat through to a study site as can the whole study system which could be considered a patch through to that of the whole globe, although more commonly a region or country (Socolar et al., 2016). Alpha-, beta- and gamma-diversity are defined in Socolar et al. (2016) as; the number of species in a patch (however that patch is defined); the difference in species composition between those patches, giving a measure of species heterogeneity and with reduction analogous to homogenisation; and the diversity of all of the patches collectively.

Unlike alpha- and gamma-diversity, beta-diversity is more complicated and therefore the particular measure of beta-diversity I have used needs a more extensive introduction. Because beta-diversity does not correspond to the diversity of a particular region (Socolar et al., 2016), multiple different ways of measuring beta-diversity have been developed. Each measure of beta-diversity has its own uses and pros and cons. These trade-offs include whether the measure of beta-diversity is independent of alpha-diversity, increases monotonically with species turnover, is bound between a sensible minimum and maximum value and is affected by differences in sampling (Barwell et al., 2015). I use beta sim in the chapters in which I model the effects of fragmentation. Beta sim is considered the best metric for presence-absence data overall and is unaffected by sample size, which I felt could be an issue as our patches got smaller with fragmentation and therefore included fewer individuals (Koleff et al., 2003; Barwell et al., 2015) (Figure 1-1).

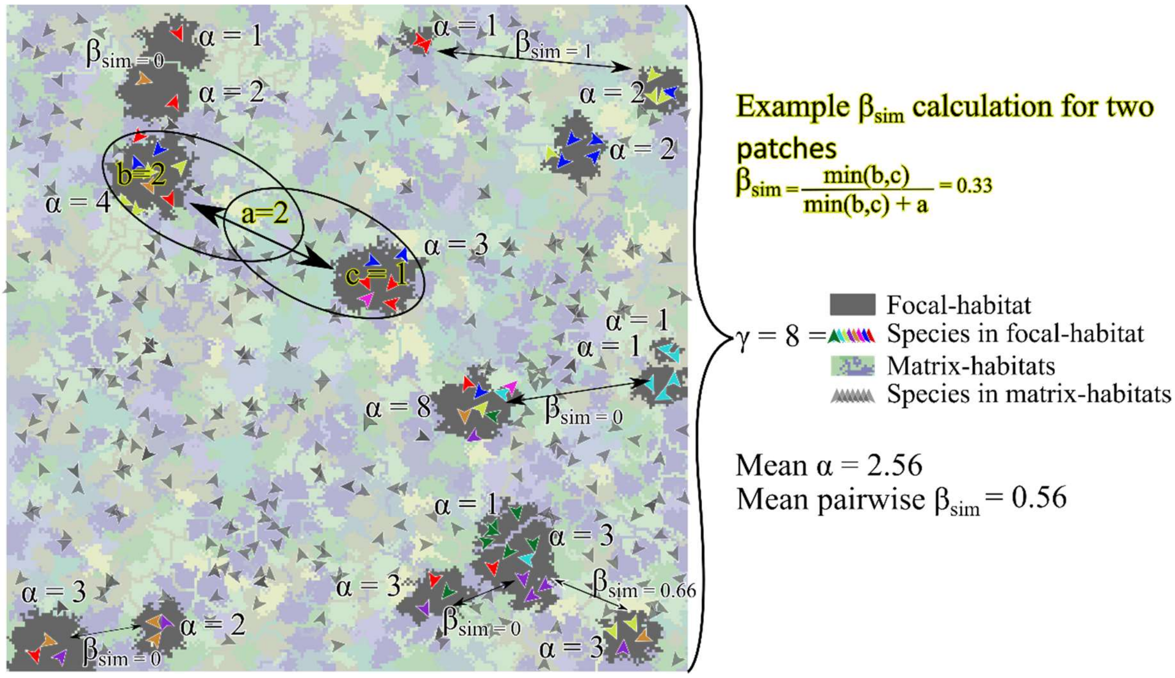

Figure 1-1 An explanation of alpha- (α), beta- (β), and gamma- (γ) diversity for species within a focal-habitat across a landscape. Beta-diversity is shown using the measure beta sim (Koleff et al., 2003) *and explained in terms of a, b and c for two patches in the middle of the landscape. a represents shared species, b species only in the left patch, and c only those in the right patch.*

Lower fragmentation might lead to higher alpha diversity of a particular patch or even the mean alpha of all the patches, simply because the average patch is bigger with less FPS (Figure 1-1). FPS creates smaller patches, which due to the *species-area relationship* and higher extinction rates, will have lower mean alpha-diversity. However, FPS may allow some rarer species to persist in some patches, leading to a greater difference in species composition between the patches and therefore a higher beta diversity. These rarer species may persist because their predators or competitors are unable to use smaller patches (Lindenmayer, 2019; Wintle et al., 2019), unable to reach isolated patches (Cartwright, 2019; Ishiyama et al., 2020) or through probabilistically not reaching a patch that they could (Glorvigen et al., 2013). Fahrig (2003) pointed out in her review that positive effects of fragmentation when controlling for habitat loss and patch isolation, such as enhanced coexistence between species and stabilisation of single-species populations, have largely been ignored. Despite Fahrig (2003) being highly cited, the situation has changed little (Fahrig, 2019). Pardini et al. (2005) showed in their study of small mammals in Brazil's Atlantic forest that an increase in fragment size and the addition of corridors to large patches led to an increase in alpha and gamma diversity, but lower beta diversity within each size category, supporting the idea of a loss of species heterogeneity. Arellano et al. (2016) used the term oligarchic species, meaning those that are abundant or common at any scale, and showed that homogenous landscapes were dominated by these oligarchic species. Decreasing fragmentation may lead to an increase in more oligarchic species and may lead to a loss of rarer species that had survived in isolated patches as they had used them as refuges from more competitive species. Of course these more ubiquitous species may be unaffected by fragmentation and reach most patches anyway, which would negate any impacts on beta-diversity. Not all species carry out the same functions in the landscape, some of these rarer species may be of benefit to the wider community, ecosystem function or to humans, by providing an ecosystem service. Ecosystem functions are generally delivered at higher levels with high levels of biodiversity as there is more chance of the species responsible for the function being conserved (Norris et al., 2011). Lower alpha-diversity has a negative effect on ecosystem function at the patch scale, but beta-diversity has been suggested as being important at a larger scale in supporting multiple ecosystem functions (Mori et al., 2018).

Thompson et al. (2019) point out how complex the issue of fragmentation is and that circumstances likely exist where fragmentation has any of positive, neutral or negative effects. There are mechanisms that could cause FPS to have a positive or negative effect on gamma-diversity. Negative mechanisms include increased patch-level extinction rates, reduced movement success between patches through the intervening land covers, the *matrix land covers*, and edge-effects (Fahrig et al., 2019; Betts et al., 2019). Positive effects could include competitive release, spreading of risk, increased functional connectivity, and higher habitat diversity (Fahrig et al., 2019; Rybicki et al., 2019). As one can see, these lists include the same or similar mechanisms leading to either positive *or* negative effects. Edge effects could have a negative effect on the fitness of species and on their occupancy through two mechanisms. First through a modifying effect on the edge of the habitat, effectively converting this area into a slightly different land cover type through changes in the microclimate and making it less suitable for those species that are most suited to core habitat (De Smedt et al., 2016; da Silva et al., 2019). And secondly through exposure to species from outside of the habitat from the matrix land covers increasing competition or predation (Wilson et al., 2014). Equally the edge could have a positive effect on some species, providing a diversity of land covers and food sources that they need, refuge from predators and therefore decreased mortality and increased movement along edges in the landscape allowing for more connected sub-populations and recolonization (Fahrig, 2017; Pfeifer et al., 2017). Additionally, the increased edge could have a positive effect through combination with the mechanism of increased matrix land cover diversity. With fragmentation, patches may be located in proximity to more kinds of matrix land covers. The increased edge also increases the interface with these matrix land covers or multiple land covers. With this increased diversity of matrix land covers, different species will be able to use the habitat that is fragmented that need access to different and now available tertiary habitat. Other paired mechanisms are those of reduced movement success *vs.* increased functional connectivity. From the perspective of a species that is strongly associated with a particular suite of habitats, grasslands for example, individuals may find it difficult to move through a non-open land cover matrix (e.g. forest) either physically or through increased mortality. However, if patches of habitat end up being closer together and more evenly spread throughout the landscape because of fragmentation, even though species may find the matrix unhospitable they will have less distance to move though unhospitable matrix and some species may be able to move between patches more easily, spending less time in the matrix. This could have potential benefits to species due to one of the other potentially positive mechanisms, the spread of risk. If all individuals of a species live in few patches of habitat, they are at risk if those patches are lost or if some threat such as disease, flood or fire increases mortality in those patches. If a species is able to inhabit more patches, that risk is reduced. Likewise, having more patches available allows competing species to occupy different patches. This is termed competitive release and results in more species coexisting within the landscape, leading to increased beta-diversity. Unfortunately, fragmentation also leads to each patch becoming smaller on average and due to the species-area relationship, these smaller patches will each be able to support fewer species, increasing patch-level extinction rates and lowering alpha-diversity.

1.2 Scale and habitat

Many empirical fragmentation studies are conducted at a patch scale, considering patches of focal-habitat that are more isolated by being further away from each other or connected through corridors of the same habitat. The surrounding or intervening land covers matrix is generally a single dissimilar and lower quality land covers type (Bender et al., 2003; Haddad et al., 2015; Haddad et al., 2017; Fletcher et al., 2018). These patch scale results could represent what happens at a landscape scale, but this should not be taken as a given as positive mechanisms of FPS may only operate at a landscape scale and extrapolation from patch scale studies to a larger scale is not the same thing as evidence at a landscape scale (Fahrig et al., 2019).Fragmentation effects should be assessed at a landscape scale (Fahrig, 2017; Fahrig et al., 2019). Fahrig's (2017) meta-analysis suggested that fragmentation may either have no effect or could have a positive effect at a landscape scale, in accord with the mechanisms described above. Fahrig (2017) did not suggest that fragmentation could have a negative effect, despite a small percentage of the studies they looked at showing this effect.

What constitutes the larger scale over which gamma-diversity could be recorded, and what scale constitutes a patch scale *vs* a landscape scale is not defined in general; simply that a landscape-scale is large (McGarigal and Cushman, 2002; Watts et al., 2016; Fahrig, 2017). Even studies that cover a larger area are often a series of patch scale experiments (Neilan et al., 2018). In these patch-scale analyses, studies measure alpha-diversity. Beta-diversity and gamma-diversity require multiple patches to be studied and are only applicable at the landscape scale. Modelling work looking at the difference in gamma-diversity with habitat area in fragmented landscapes led to the *species-fragmented area relationship* (SFAR) as a modification to the *species-area relationship* when landscapes are fragmented (Hanski et al., 2013). Hanski et al. (2013) showed that gamma-diversity is lower than it would be in a contiguous equivalent area because of the negative effects of fragmentation causing alpha-diversity to be lower in each patch. This study, along with patch scale studies, did not account for beta-diversity however, and the positive effects fragmentation may have on this through the previously mentioned competitive release, positive edge effects and increased land cover diversity.

Patches over which alpha-diversity, or multiple patches over which beta- and gamma-diversity are measured, are typically of a single habitat type. The habitat of a species is related to its Grinnellian niche (Devictor et al., 2010). The niche for animal species is the envelope of climatic and other abiotic, both micro and macro scale, suitability and range of biotic interactions with food sources and predators. These niches may vary throughout an organism's life and seasonally, with species sometimes needing different resources to reproduce or relying on different resources. Despite the range of the niche and therefore differences in what constitutes habitat, information on the habitats of a particular species is often derived from expert opinion, small scale analysis and limited to a single or few land covers (Lonsdorf et al., 2009; Ball et al., 2013; De Lima et al., 2016; Webb et al., 2017; Ferrão et al., 2018). Human-perceived land cover types are often wrongly assumed to be the habitat for multiple sorts of species, even though it is well known that different species may use part of, or multiple land cover types (Betts et al., 2014; Halstead et al., 2019; Valente and Betts, 2019). Instead of thinking of a species belonging to a particular land cover, it may, therefore, be more appropriate to consider a species-level perspective at the scale of a study (Betts et al., 2014). This has important implications for how fragmentation is modelled, as a species may be able to live in several land covers, and so models may need to represent multiple different land covers. These multiple land covers also allow for the capturing of the positive mechanism of increased land cover diversity with fragmentation, with new patches interacting with more land cover types and therefore allowing more species, with different requirements. Specialists and generalists are often defined by an association with a particular land cover or with many respectively, but this association is open to interpretation (Da Silveira et al., 2016). Being a generalist does not mean the species does not have land cover preference (Townsend et al., 2008; Da Silveira et al., 2016). Specialists are considered to be more competitive in a preferred or more suitable land cover compared to a competitively inferior generalist in that land cover, but the generalist more competitive in general across multiple land covers (Marvier et al., 2004). Specialist species associated with a land cover are often considered to be negatively affected by FPS (Kosydar et al., 2014; Fahrig, 2017) and that where FPS has been shown to be positive that this is because generalists increase (Hu et al., 2012). However, Fahrig (2017) found that FPS had a positive effect on the landscape-level species richness of specialist, rare, or threatened species in 97% of the studies they looked at. Is this because FPS allows for separation of otherwise competing species among patches of the focal-habitat within the landscape (Ramiadantsoa et al., 2018)?

As well as having different sorts of land cover requirements, species move around landscapes differently. This may include the allocation of different resources to dispersal structures, such as larger legs or wings (Bonte et al., 2012). Species or even individuals within species may have different dispersal abilities (wing dimorphism for example), and individuals with features that enhance movement may be more common in fragmented landscapes (Cote et al., 2017). Individuals or species may also show variation in boldness, being more or less likely to move between patches (Fraser et al., 2001). Historic exposure to fragmentation has led to landscapes containing species adapted to fragmentation and more able to move through fragmented landscapes (Betts et al., 2019). It is likely, therefore, that different studies would contain species that move differently and therefore studies showing positive effects of fragmentation could be because these landscapes contain more fragmentation adapted species.

1.3 Simulations and Individual-based Models

Simulations are useful as they allow us to pull apart complex situations, investigating a problem in ways that would otherwise be impossible or extremely difficult. They allow for the separation of intrinsically linked traits of a species or the environment. They can be used where field studies would be extremely difficult in terms of the scale of analysis, requiring huge amounts of time, money and people to investigate. Agent-based models, often called *individual-based models* (IBMs) in ecology, allow for simulation of the wider system by looking at the emergent properties arising from the individual action of an agent, in the case of ecology most often an individual or small group of individuals, called a super-individual, of a species (Grimm and Railsback, 2005). Traditional models have been shown to sometimes be wrong because they are too simple and leave out the action of individuals (Railsback and Grimm, 2017). In the case of habitat fragmentation or connectivity deterministic analysis would also become impractical as the number of patches increased to high numbers and with the complexity of different land covers of different shapes in the matrix between the fragmented land cover type (Kanagaraj et al., 2013). IBMs take small scale analysis of a species or an environment to program in the behaviour of individuals of a species. These individuals then interact with other individuals, either of its own or another species, and the environment often in a spatially-explicit manner. The simulation can then be used to set up new, "virtual", experiments to investigate a theoretical question or to inform practical conservation management (DeAngelis and Grimm, 2014). Even if the simulations are not sufficient in answering a question fully, they can be useful to test theoretical concepts and as a beginning point for future lab or field-based analysis. IBMs have been used specifically to explore fragmentation using specific species (Jepsen and Topping, 2004; Lasky and Keitt, 2013) and by using generic species (Fahrig, 2001; Rybicki et al., 2019). Generic species are those which have general characteristics to allow for exploration of ecological principles (Jepsen et al., 2005).

1.4 Research questions and thesis structure.

To explore general theoretical effects of FPS on biodiversity I chose not to focus on any particular group of species; instead focusing on generic species and using values that would be applicable to multiple species types at different spatial and temporal scales. Using generic species allowed for generalisability of my results and exploration of theoretical possibilities (Simpkins et al., 2018). It was important to ground these generic species within the realm of characteristics of real species. As is common practice in IBMs I used allometric equations to give appropriate values to the generic species we used (Sibly et al., 2013). The values I used could scale to 5 m per minute and 260 offspring a year for invertebrates if I considered the cell size to be a metre and our time step of a minute, or 5 km per hour and four offspring a year roughly equivalent of birds or mammals if the cell size was a km and the time step equal to an hour. I created a multi-species and landscape-scale IBM and generated simulated landscapes that allowed for control over fragmentation and the land covers between patches, *matrix land covers*, of this fragmented habitat, the *focal-habitat*, while controlling for the focal-habitat area.

Real landscapes have a high correlation between habitat amount and configuration (Fletcher et al., 2018). Therefore, in simulation studies, landscapes are frequently simulated using different methods. These can be a fractal generation (Spanowicz and Jaeger, 2019; May et al., 2019), random clustering using probability (Saura and Martínez-Millan, 2000), or by sampling real landscape features and tiling to create new landscapes of approximately the right configuration (Gunton et al., 2017). Some of these land cover generation methods involve specifying fragmentation using non-direct methods such as exponents which are not directly relatable to the number of patches (Spanowicz and Jaeger, 2019). These methods also create binary land covers. In this thesis, I instead opted to create my own land cover generator based solely on the number of patches and area and specifically designed to allow for multiple matrix land covers and to consider FPS explicitly (Figure 1-1).

As part of the process of creating a simulation, to address the issue that species are not associated with a single land cover, I conduct an analysis of the habitat association of species, applying a new methodology to a case study of ground beetles (Carabidae). This first research chapter (chapter 2) of the thesis does not directly answer questions related to fragmentation but was instrumental in the development of the IBM in which multiple species coexist due to having different suitabilities and preferences for the land covers of the simulated landscapes. The analysis also gives greater insight into the concept of a species-level perspective. This chapter develops an improvement on a method used in plant science, the phi coefficient of association, to make it more useful for looking at the habitat association of mobile species or when using data with a level of uncertainty. I then use this method to answer the first research question of the thesis; how do species relate to different land cover types? This analysis directs the development of the simulation, with species defined as each being more or less associated with different land cover types in their own specific manner. Doing so also allows me to implement a species-level perspective into my IBM.

The latter chapters all use the same IBM with different parameters and configurations of the land cover. Chapter 3 is an ***O****verview,* ***D****esign concepts,* ***D****etails* (ODD) (Grimm et al., 2006; Grimm et al., 2010) used to describe the common IBM used for chapters 4, 5 and 6. The first of the simulation chapters looks at the different effect fragmentation has on species with different specialisms, habitat dependencies and corresponding competitive abilities compared to a model in which species have no difference in land cover suitability. The second simulation chapter (chapter 5) looks at the effect the matrix and the use of extreme binary landscapes have on studies of fragmentation. The third simulation chapter (chapter 6) compares more complex movement modes to the random-walk used in the previous chapters and manipulates how long individuals spend in the matrix and how readily they move between focal-habitat patches by varying the strength of the effect of bias towards more suitable land cover and how directly species move through the matrix land covers.

During the debate on the effects of habitat fragmentation, Fahrig (2017) found that a majority of examples within their analysis showed either a neutral or positive effects of fragmentation on biodiversity at the landscape scale. Therefore, I use the simulation to answer whether; alpha- and gamma-diversity always decline and beta-diversity increase with FPS? Fahrig (2017) then gave some summarised examples from across the literature as to why authors thought that fragmentation may be showing the unexpected non-negative result. These included that generalists species are driving the increase, although Fahrig (2017) pointed out that in the studies they considered, the positive effect was also seen for specialist, rare or threatened species. Therefore, I investigate; whether specialist and generalists increase or decrease in gamma-diversity with FPS? However, simply looking at whether a species' specialism, in general, leads to differences in the effect FPS has, does not take into consideration the identity of the species in terms of their association with the focal-habitat that was fragmented (Fletcher et al., 2018). With this in mind, I also investigate; if these increases or decreases universal for all species, or are species that are dependent on the focal-habitat affected differently?

In chapter 4 I answer the above three question. I start by looking generally at the effect of land covers having different suitability for the species within the landscape, comparing a model without land cover suitability, with species moving entirely randomly around the landscape, to one where species have decreased mortality in more suitable land cover and a preferential movement towards more suitable land cover. I then further modify this latter model by making half of the species specialists and the other half generalists. The effect of FPS is looked at for all species in the focal-habitat, and then in three groups, those for whom the focal-habitat is highly, moderately and least suitable. I conduct this analysis on landscapes that contained eleven land covers, a focal-habitat, and ten other land covers.

A few empirical studies have looked at the effects of the matrix on fragmentation, but in these cases, they only looked at a few matrix land covers and then each individually in combination with the focal-habitat at a patch scale (Sisk et al., 1997; Hatfield et al., 2019). As species interact differently with different matrix land covers (Haddad et al., 2017; Fletcher et al., 2019; Thompson et al., 2019) and have different habitat preferences (Bollmann et al., 2005; Chetcuti et al., 2019) it is important to investigate the effect of FPS on biodiversity with different configurations of the matrix (Fahrig, 2017; Fletcher et al., 2018). In chapter 5, I vary the matrix land covers and investigate the overall question of; how the structure of the land covers in the matrix between a focal-habitat affect the relationship of diversity in the focal-habitat to fragmentation per se? I do this because many of the empirical and modelling studies conducting fragmentation and connectivity analysis use binary-landscapes containing only a focal-habitat that is fragmented and a matrix land cover (Ewers et al. 2011, Haddad et al. 2017, Damschen et al. 2019, Thompson et al. 2019, May et al. 2019). I therefore answer the sub-question; does using binary landscapes with the matrix represented by one low quality land cover vs. more matrix land covers affect the relationship between fragmentation and biodiversity? These landscapes are also usually designed or chosen to maximise the contrast between the focal-habitat and the matrix, by choosing a species-poor and very different matrix land cover in comparison to a richer focal-habitat, for example, a woodland focal-habitat and an arable matrix (Crawford et al., 2016). Therefore, I also answer two sub-questions; 1) How does species diversity responds to fragmentation per se when the matrix land covers are associated with more (high quality land covers) or fewer (low quality land covers) species? And; 2) how does species diversity responds to fragmentation per se when the matrix land covers are more (broadleaf to conifer and scrub, or unimproved grassland to different grasslands, for example improved grassland) or less similar (woodland to grassland or vice versa) to the focal-habitat? I answer these questions by varying the number of matrix land covers. I also include two scenarios varying the type of matrix. The first of these varies how similar or dissimilar the matrix land covers are to the focal-habitat. The second scenario varies how many species depend on each of the matrix land covers compared to the focal-habitat.

It has been suggested that fragmentation could have different effects on different sorts of species. The species that spend more time in the matrix would likely be more negatively affected by fragmentation while species that are able to traverse between patches of focal-habitat and for whom more fragmented landscapes may be functionally more connected, may benefit from FPS (Fahrig, 2017). I therefore investigate; if species that spend more time in the matrix decline in species diversity in the focal-habitat with increasing fragmentation per se of the focal-habitat compared to species that spend less time in the matrix? And whether; species that have a higher encounter rate with patches of focal-habitat, increase in species diversity in the focal-habitat with fragmentation per se of the focal-habitat while species with lower encounter rates increase less or decline? In designing species that are able to traverse between patches it is important to look at how species move. Studies have simulated species that move with a *random walks* (RWs) as I do in the two preceding fragmentation chapters (Fahrig, 2001; Rayfield et al., 2011) and with *correlated random walks* (CRWs) (Johnson et al., 1992; Boone and Hunter, 1996; Jepsen and Topping, 2004; McIntire et al., 2013). These are often criticised as being unrealistic, as species sometimes move differently depending on the land cover they find themselves in (Kuefler et al., 2010), and therefore moving with *habitat dependent walks* (HDWs). Each walk is likely specific to a different sort of species (Da Silveira et al., 2016; Thomaes et al., 2018; Bérces and Růžičková, 2019; Fletcher et al., 2019). I assume that studies of fragmentation showing different overall trends likely contained different proportions of species moving with different walks. In the last research chapter of my thesis (chapter 6), to investigate difference in encounter rate I change the walk of the species to be either a RW, HDW and CRW and to vary the time spent in the matrix I change the bias towards more suitable land cover.

My thesis uses a species-level perspective of landscapes and different sorts of generic species with the aim of consolidating the opposing positions of the fragmentation per se debate. By using generic species, I hope to find general relationships and do not seek to find relationships specific to different genera or species. Initially I explore how suitable different land covers are for species. I then use the perspective of species finding different land covers to be differently suitable in my individual-based model, to explore how the effect of FPS may differ under different circumstances. I look at the effect of FPS on species with differing specialism and habitat association, the effect of the matrix land covers and finally at species with different levels of site fidelity and ability to traverse the landscape.

Chapter 2

A weighting method to improve habitat association analysis: tested on British carabids

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2.1 Abstract

Analysis of species' habitat associations is important for biodiversity conservation and spatial ecology. The original phi coefficient of association is a simple method that gives both positive and negative associations of individual species with habitats. The method originates in assessing the association of plant species with habitats, sampled by quadrats. Using this method for mobile animals creates problems as records often have imprecise locations, and would require either using only records related to a single habitat or arbitrarily choosing a single habitat to assign.

We propose and test a new weighted version of the index that retains more records, which improves association estimates and allows assessment of more species. It weights habitats that lie within the area covered by the species record with their certainty level, in our case study, the proportion of the grid cell covered by that habitat.

We used carabid beetle data from the National Biodiversity Network atlas and CEH Land Cover Map 2015 across Great Britain to compare the original method with the weighted version. We used presence-only data, assigning species absences using a threshold based on the number of other species found at a location, and conducted a sensitivity analysis of this *threshold. Qualitative descriptions of habitat associations were used as independent validation data.*

The weighted index allowed the analysis of 52 additional species (19% more) and gave results with as few as 50 records. For the species we could analyse using both indices, the weighted index explained 70% of the qualitative validation data compared to 68% for the original, indicating no accuracy loss.

The weighted phi coefficient of association provides an improved method for habitat analysis giving information on preferred and avoided habitats for mobile species that have limited records, and can be used in modelling and analysis that directs conservation policy and practice.

Key-words: carabids, Coleoptera, ground beetles, habitat classification, habitat preference, invertebrate, land cover, site fidelity, phi coefficient of association

2.2 Introduction

Habitat association analysis is used in determining the likely habitat requirements of individual species (Cole et al., 2010). These requirements are important, for example, in studying impacts of habitat loss and fragmentation (Maclean et al., 2011), dispersal and habitat connectivity (Brodie et al., 2016), and modelling foraging and movement over landscapes, such as in pollinator models (Lonsdorf et al., 2009) and conservation prioritisation (Pouzols and Moilanen, 2014). Such analyses are particularly important when planning landscapes for conservation: for example, in assessing the impact of adding a patch of habitat for certain species, it is also necessary to understand which species avoid that habitat. Lawton et al. (2010) highlight that the approaches available for designing ecological networks are limited by the availability of evidence, usually using expert consensus. Habitat association analysis contributes to this evidence base.

Searching the literature for habitat association or preference returns many examples of species distribution models (SDMs) and indicator species analysis. Examples of analysis looking at preference of a species to each of several alternative habitats are returned less often. For example, SDMs predict where species are likely to be found within a landscape, with habitat type being only one factor (De Lima et al., 2016). Indicator species analysis identifies species that best represent a habitat or group of habitats, and is used in monitoring habitat condition (Hill et al., 1975; De Gasperis et al., 2016). Direct analysis of which habitats a species prefers and which it avoids, which is particularly useful in conservation planning, are few. In this paper, we consider a direct approach to determine habitat association, which comprises the relative preference of a species for multiple habitats.

Information on habitat associations is generally derived from expert knowledge (Lonsdorf et al., 2009) or analysis over a small geographic area (Ball et al., 2013; De Lima et al., 2016; Ferrão et al., 2018) and is often limited to associations with a single habitat or a few broad habitats (Webb et al., 2017). Large-scale analysis of habitat association de-emphasises the less frequent recordings of a species in a habitat in which the species is transient, which could be misconstrued at a small-scale as association. Although SDMs (Petit et al., 2003; Phillips et al., 2006; Porto et al., 2018) and indicator species analyses (Hill et al., 1975; Gardner, 1991; Ricotta et al., 2015) are often done over large scales, this is rare for analysis of the preference of a species . Exceptions are Eyre and Luff (2004), who used ordination to study habitat preferences of carabids in North East England and the Scottish Border, and Redhead et al.(2016) who used general linear mixed effects models to study butterfly habitats across Britain.

Eyre and Luff (2004) used ordination in a straightforward way, giving each carabid species a weighted average from positive to negative for each habitat. They did, however, point out that care should be taken in interpreting their findings due to some anomalous results. Redhead et al. (2016) used the coefficients from their model to derive associations. Their method worked well, albeit with large variation in the associations within individual species, but needed approximately 5000 records to ensure accuracy. They used this approach, as other methods required more precise locations information than the 1 km they used.

De Cáceres and Legendre (2009) created a framework for ecologists explaining when to use IndVal or an alternative, the Phi coefficient of correlation (Pearson, 1896). We focus in this paper on the Phi coefficient of correlation, ("correlation index") which like IndVal is simpler than ordination. Unlike IndVal, the correlation index gives a negative association value when a species appears to avoid a habitat, and uses species' absences to provide extra information (De Cáceres and Legendre 2009). The Phi coefficient gives degree of preference for a habitat compared to other groups. By contrast IndVal assesses how much the target site group matches a set of sites where the species is found and is an indicator species analysis. The correlation index was created by Karl Pearson (1896) and at its simplest is the binary version of the Pearson's correlation (De Cáceres et al., 2008). It is the preferred method in plant science for calculating site fidelity (De Cáceres and Legendre, 2009), but has not been adopted more generally despite De Cáceres and Legendre's (2009) framework. The index uses two binary vectors to describe a location: one representing presence or absence of the species and the other whether a location is the habitat of interest. The index does not incorporate uncertainty in the habitat of the location, it is either habitat or not. Species records often have a degree of uncertainty, particularly concerning the spatial resolution of the record. The area covered by the resolution of the record may contain multiple habitats. The binary nature of the correlation index requires either removal of mixed or uncertain habitat data or a judgement as to which habitat to assign. While this might be considered as an error in the record, movement of individuals from preferred into adjacent less-preferred habitats is common (Ries et al., 2004), and so the precise location in which a mobile individual is found may not be in a preferred habitat. To incorporate these issues, we propose a new version of the correlation index, adding a third vector to each record, which is a weighting based on the certainty of the habitats at a location. We present the weighting as the proportion of a particular habitat in 100 m grid cell. However, the weighting could be the probability of correctly classifying a habitat from remote sensing or a combination of weightings.

In this paper, we present our weighted version of the correlation index and test it against the original version using a case study of carabid beetles of Great Britain. We also carry out a partial validation of the correlation indices using qualitative data from species descriptions. The analysis uses records from the UK National Biodiversity Network (NBN) Atlas (2018) and Centre for Ecology and Hydrology (CEH) Land Cover Map 2015 (LCM2015) (Rowland et al., 2017a). We used a method that considers the number of other species within the family found at a location as proxy for survey effort (Hickling et al., 2006; Redhead et al., 2016). We use an absence threshold of 14 carabid species and conduct a sensitivity analysis of the threshold value. Most species have fewer than 1000 records. We, therefore, ascertain how many records are required to give a valid estimate of habitat association.

2.3 Methods

2.3.1 Correlation indices

The original correlation index uses binary presence-absence with each location assigned to one group (habitat) (De Cáceres and Legendre, 2009). The index is the Pearson correlation coefficient for two binary vectors with length L, one vector representing the species presence/absence at each location ($\boldsymbol{s}$) and another representing if each location is the habitat of interest ($\boldsymbol{h}$) (De Cáceres and Legendre, 2009). The lengths and sums of each vector are used in equation (2-1

$$\Phi = \frac{N \times n_p - n \times N_p}{\sqrt{(N \times n - n^2) \times (N \times N_p - N_p^2)}} \tag{2-1}$$

Where N is the total number of locations ($N = L$), N_p the number of locations with the habitat of interest ($N_p = \sum_{i=1}^{\mathrm{L}} h_i$), n is total number of occurrences across all locations ($n = \sum_{i=1}^{\mathrm{L}} s_i$), and n_p is the number of occurrences in habitat of interest ($n_p = \sum_{i=1}^{\mathrm{L}} h_i s_i$). In the event that a location is not a point location and instead covers an area, a location could contain more than one habitat. For example, in location 4 (Table 2-1), an area location contains acid grassland (2%), inland rock (59%) and heather (39%). We do not know in which habitat the species was found, therefore when calculating the original index, either only locations that contain a single habitat could be included or a habitat would need to be chosen. We might choose to discard all locations with more than one habitat. This would leave locations 1, 2, 3, 5, and 7 in Table 2-1. The carabid species of interest is then either present or absent within that single land cover type. Using this approach can remove a large proportion of the data, sometimes making a species unviable for analysis. Another way of conducting the unweighted analysis would have been to choose the habitat covering the largest proportion of the 100 m location; a version of the analysis doing this can be found in Appendix C2.1. To allow the use of a larger proportion of the data, we created a weighted version of the index (equation (2-2).

$$\Phi^{w} = \frac{N \times n_p^{w} - n \times N_p^{w}}{\sqrt{(N \times n - n^2) \times \left(N \times N_p^{w} - N_p^{w2}\right)}} \tag{2-2}$$

Table 2-1 Example of the vectors that can be used in calculating the Phi coefficient for each individual habitat, showing the , proportion of each habitat within each location and the binary presence data, in this case for the species Abax parallelepipedus (see Appendix 2 for matrix version of this information and equations).

Location ID	**LCM2015 habitat**	**Heather habitat vector (h)**	**Weight vector (w)**	**Species vector (s)**
1	Heather grassland	0	1.00	0
2	Supralittoral sediment	0	1.00	0
3	Heather grassland	0	1.00	0
4	Acid grassland	0	0.02	1
4	Inland rock	0	0.59	1
4	Heather	1	0.39	1
5	Inland rock	0	1.00	0
6	Heather	1	0.76	0
6	Improved grassland	0	0.24	0
7	Inland rock	0	1.00	1
…	…	⋮	⋮	⋮

All three vectors have length L

This version added a third non-binary vector of the weighting of each habitat at each location ($\boldsymbol{w}$). This weighting could be any by which each location sums to one (for example land cover classification certainty) but we used the proportion of each habitat. All three vectors have length L. N is still the total number of locations ($N = \sum_{i=1}^{\mathrm{L}} w_i$), and n is still the total number of occurrences across all locations ($n = \sum_{i=1}^{\mathrm{L}} w_i s_i$). The values of N and n are the same as they would be if each of the locations only had a weighting of one (a single habitat in our example). The N_p and n_p values change however, now denoted as N_p^w and n_p^w. These can be calculated as $N_p^w = \sum_{i=1}^{\mathrm{L}} w_i h_i$ (lower than a hypothetical N_p would be) and $n_p^w = \sum_{i=1}^{\mathrm{L}} w_i h_i s_i$(smaller than a hypothetical n_p). So for only the data in Table 2-1 (assuming no threshold was applied) and with Inland rock being the habitat of interest; $n_p^w = 0.59 + 1 = 1.59$, $N_p^w = 0.59 + 1 + 1 = 2.59$, N = 7 and n = 2 and therefore using the equation for the weighted correlation index (equation (2-3) gives;

$$\Phi^w = \frac{7 \times 1.59 - 2 \times 2.59}{\sqrt{(7 \times 2 - 2^2)(7 \times 2.59 - 2.59^2)}} = 0.56 \tag{2-3}$$

The weighted version balances the reduced terms n_p^w in the numerator of the equation with N_p^w in the numerator and denominator meaning the equation still gives both positively and negatively correlated habitats. If all of the locations within the analysis are certain (one habitat), the weighting is 1 and the result is the same as the original correlation index. See Appendix 2 for matrix representation of the data and other equations.

We calculated both the original and the uncertainty-weighted correlation index ϕ values and permutated (De Cáceres and Legendre, 2009) to get a p-value for each habitat and for each carabid species. See De Cáceres and Legendre (2009) for additional considerations when conducting permutation tests.

2.3.2 Data

We used the large volume of carabid (Coleoptera: Carabidae) location records and high-quality land cover data available in Great Britain.

2.3.2.1 Carabid data

The National Biodiversity Network (NBN) atlas (2017) contains presence records for many species, at 100 m resolution resulting from the six digit Ordnance Survey grid reference (Telfer, 2006). We downloaded all records of carabid locations from the NBN atlas on the 7/11/2017 and initially selected those above an arbitrary threshold of at least 10 records (268 species). We converted the coordinates into 100 m grid cells, with the coordinates representing the bottom left corner, using ArcGIS (v 10.4.1 © 2016 ESRI, Redlands, California). NBN species names were checked and synonyms corrected using the Natural History Museum UK species inventory checklist (Raper, 2014). Remaining synonyms were corrected using the checklist in Luff (2007). These steps increased the number of records for species with accepted names on these checklists.

The NBN does not include absence data. A species cannot be considered to be absent from all locations where it is not recorded. To allow us to have confidence that a species was genuinely not at a particular location, we counted the number of other species found in each location as a measure of survey effort. Following Hickling et al (2006) we considered a location to be a true absence if it had more records than a threshold number of other carabids. The threshold number of species is arbitrary. For butterflies, Redhead *et al.* (Redhead et al., 2016) used a value of 10%

of the species pool (5 species). Using 10% of the carabid species would have required 28 or more species, giving only 94 locations across Britain. We used a threshold of 14 species (5%) giving 556 potential absence grid cells and conducted a sensitivity analysis of this value. Absence locations for a species are the remainder of these 556 grid cells after removing those containing the species of interest.

2.3.2.2 Land cover

We used the vector LCM2015 for Great Britain (Rowland et al., 2017a) to provide habitat data. LCM2015 contains 21 land cover classes based on the UK Biodiversity Action Plan Broad Habitats (Jackson, 2000). These classes are assigned to Ordnance Survey Master Map polygons using a Random Forest object-based classification of satellite Landsat-8 (30 m resolution) and AWIFS data (60 m resolution) (Rowland et al., 2017b). Polygons smaller than 0.5 ha or less than 50 m in width are merged into neighbouring polygons. This can remove linear habitats such as those within freshwater, only capturing larger water bodies and wide rivers (Rowland et al., 2017b).

We intersected LCM2015 data with the 100 m NBN squares and calculated the proportion of each habitat at each location. In principle, one might include temperature or altitude, or group land cover classes. Analysing a large number of alternative habitats can lead to a loss of power. Therefore, if dividing some habitats, others should be amalgamated. But here, for simplicity, we used the LCM2015 classes as they are without further classification.

2.3.3 Validation data

To allow validation of both weighted and original correlation indices we used information from Luff, (2007) "*The Carabidae (ground beetles) of Britain and Ireland"*. Luff (2007) is a comprehensive text on British carabid identification including descriptions of where the species might be found. We used only habitat preferences within the British Isles due to differences in associations to other parts of Europe (Eversham and Telfer, 1994; Desender et al., 2005). Luff, (2007) stated the preferred habitat for each carabid species in a descriptive way; for example, "In most habitats, especially agricultural fields, gardens and other disturbed, open and dry situations" (p. 68, *Trechus quadristriatus*). Luff (2007) did not create the book as a database of species associations. It was, therefore, necessary to convert the text into a database against which we could compare our analyses.

We developed a method using as little subjective interpretation as possible. We looked at all words in the descriptions in Luff (2007) of habitat and picked out those words naming a habitat. We then translated these, into either an individual or group of LCM2015 habitat classes. For example, "moorland" in Luff was translated as including Inland rock (in LCM2015 documentation included under "Mountain, heath, bog" (Rowland et al., 2017b)), Acid grassland, Heather grassland, and Heather & Bog. Where Luff's habitat descriptions represented a group of land covers, the group was included in the database as an aggregate class against which to check the analysis. For a table showing a full list of the words used and resulting LCM2015 habitat classes and aggregates (see Table A C2.1).

2.3.4 Analyses

The NBN data contained a separate record for each species at each relevant 100 m location meaning that individual locations appeared multiple times. We created a version of the data with each location represented once, giving presence or absence (absences determined as described above) for each species at that location. We created this wide format version by using an R script to go through each location and assign a new binary column of presence for each species. Table 2-1 shows an example of the data after pre-processing. The correlation index and permutations of the analysis, for each species and versions of the method, were processed using the JASMIN cluster (Lawrence et al., 2013). The R scripts for all analyses can be found in the supplementary materials of the published paper.

2.3.4.1 Sensitivity analysis

We conducted a sensitivity analysis of threshold number of species used to define absence locations by using Spearman's rank correlation to determine to what extent the order of the habitat associations from positive to negative ϕ changed using seven (2.5% of the total species number) and 28 (10%) species number thresholds compared with the baseline of 14 . We also compared the order of habitat associations from positive to negative ϕ between the weighted and original index for each species using Spearman's rank correlation.

2.3.4.2 Validation

The correlation index results for each carabid species were validated by comparing them to the database created from Luff (2007) (section2.3.3). For each species, we calculated the percentage of "Luff habitats" that were also found to be significantly (p-value $\leq$ 0.05) and positively associated habitats in our correlation analysis for that species.

2.4 Results

By allowing the use of locations containing more than one habitat, the weighted index used more records for each species and therefore included 52 extra species; 19% more. For example, for *Bembidion prasinum* the original method only included 14 records, but the weighted method used 79 records. Luff (2007) describes this species as living in shingle near running water. The original method did not include freshwater at all due to a lack of records. The weighted method associated the species most strongly with freshwater. Comparing the rank of the habitats based on their Phi score for the weighted and original analyses for this species using Spearman's rank, the rho value was only 0.62. The species that have far fewer records in the original than the weighted version, like *B. prasinum*, drove the average correlation down. In most cases where both species had many records, the rank correlation was higher. One exception to high correlation with many records is *Curtonotus aulicus* that had 106 original and 258 weighted records. The original version had freshwater non-significantly (p = 0.392) positive despite this being described as a dry habitat species (Luff, 2007). The weighted analysis of *C. aulicus* had freshwater as the habitat most significantly ($p = 8.00 \times 10^{-04}$) avoided.

2.4.1 Validation

Using the 14 species threshold for absence, the original version had 207 and the weighted version 264 species with at least one significant habitat association. Furthermore, the weighted and original indices gave similar ranked habitat associations, with the average Spearman's rank correlation 0.82 (SE 0.008) between the two indices. That is not to say however, that significant results sensibly described the habitat of the species. We, therefore validated the correlation results against the database created from Luff (2007).

Considering the average (across species) percentage match of our analyses to Luff habitats, the original analysis identified on average 68% (using 187 species) of Luff habitats and the weighted analysis 70% (using 239 species). This is not a great deal more on average, but does include more species. In the original version, all of the Luff habitats were identified for 94 species and at least one Luff habitat for 157 species. In the weighted analysis, all of the Luff habitats were selected for 126 species and at least one Luff habitat for 205 species. Comparing with Luff (2007), the weighted version matched 18 species less well than the original version, 141 matched as well, and 28 matched better. Overall, using only the species analysed using both methods, the weighted version matched 6.8% on average better compared to the original version. Figure 2-1 shows the graphical comparison of the two versions of the index. The weighted version generally gave a slightly higher percentage matches for species with a moderate to large number of records, and included more species with few records.

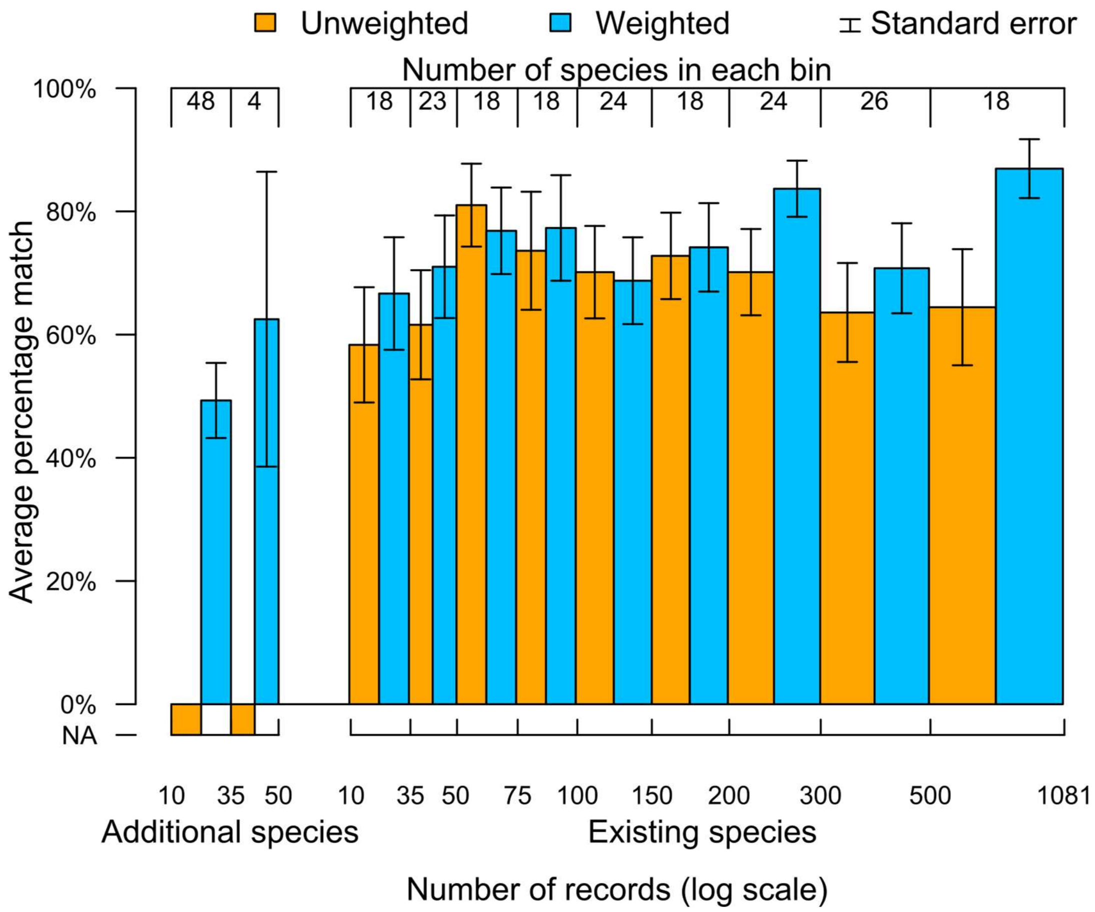


Figure 2-1 Comparison of original and weighted correlation index showing how they match the validation data. Species are in bins of the number of records (using the records without removal, as used in the weighted version). Species that did not have enough records in the original version are included on the left to show that the weighted version on average when including these species achieves a match with the validation data.

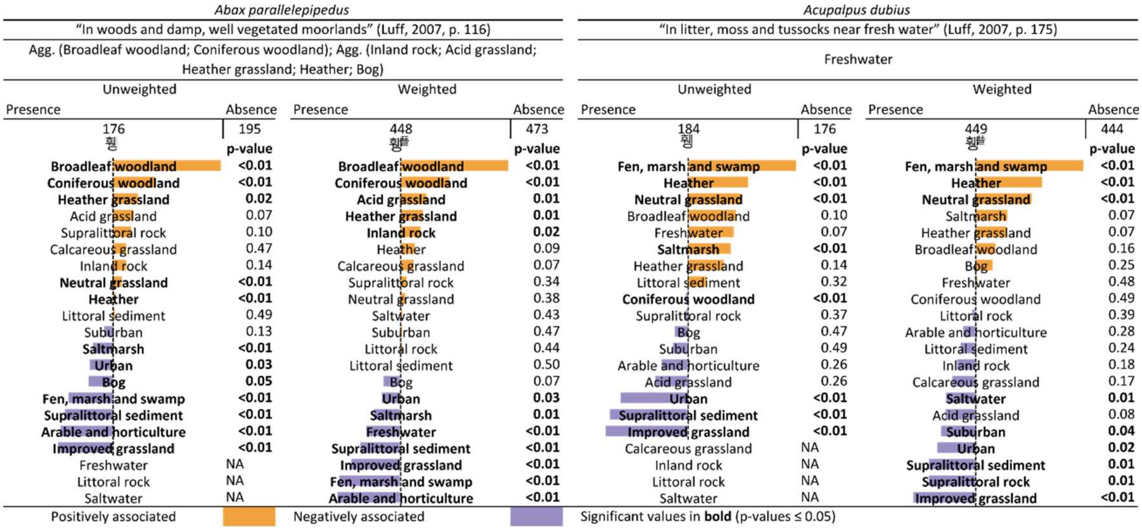
2.4.2 Individual species examples.

Here we give examples showing comparisons between the original and weighted version of the index, the improvement using the weighted method and establishing how few records are required to give a reasonable estimate of habitat preference. For the full dataset of all carabids analysed see Appendix 4.

2.4.2.1 Original vs weighted index

Abax parallelepipedus is described by Luff (2007) as a woodland and moorland species. Due to insufficient data, the original version failed to classify three habitats, despite having 176 records, but did show a preference for woodland and heather grassland (Figure 2-2). The weighted method classified all habitats and captured the woodland and more of the moorland habitat types. For *Acupalpus dubius* neither analysis matched Luff ("In litter, moss and tussocks near fresh water"(p.175) translated as Freshwater), but may give additional information (Figure 2-2) as an association was found with "Fen, marsh and swamp", potentially represent the moss and tussocks of Luff's description. The analyses identifies freshwater for other waterside species (see Appendix 4), this therefore is not a consistent problem with detecting freshwater.

Two examples are; *Anthracus consputus* and *Trechoblemus micros,* which both Luff and our analysis classify as freshwater species.



Abax parallelepipedus

"In woods and damp, well vegetated moorlands" (Luff, 2007, p. 116)

Agg. (Broadleaf woodland; Coniferous woodland); Agg. (Inland rock; Acid grassland; Heather grassland; Heather; Bog)

Unweighted: Presence 176	Absence 195 p-value	Weighted: Presence 448	Absence 473 p-value
Broadleaf woodland	**<0.01**	**Broadleaf woodland**	**<0.01**
Coniferous woodland	**<0.01**	**Coniferous woodland**	**<0.01**
Heather grassland	**0.02**	**Acid grassland**	**0.01**
Acid grassland	0.07	**Heather grassland**	**0.01**
Supralittoral rock	0.10	**Inland rock**	**0.02**
Calcareous grassland	0.47	Heather	0.09
Inland rock	0.14	Calcareous grassland	0.07
Neutral grassland	**<0.01**	Supralittoral rock	0.34
Heather	**<0.01**	Neutral grassland	0.38
Littoral sediment	0.49	Saltwater	0.43
Suburban	0.13	Suburban	0.47
Saltmarsh	**<0.01**	Littoral rock	0.44
Urban	**0.03**	Littoral sediment	0.50
Bog	**0.05**	Bog	0.07
Fen, marsh and swamp	**<0.01**	**Urban**	**0.03**
Supralittoral sediment	**<0.01**	**Saltmarsh**	**0.01**
Arable and horticulture	**<0.01**	**Freshwater**	**<0.01**
Improved grassland	**<0.01**	**Supralittoral sediment**	**<0.01**
Freshwater	NA	**Improved grassland**	**<0.01**
Littoral rock	NA	**Fen, marsh and swamp**	**<0.01**
Saltwater	NA	**Arable and horticulture**	**<0.01**

Acupalpus dubius

"In litter, moss and tussocks near fresh water" (Luff, 2007, p. 175)

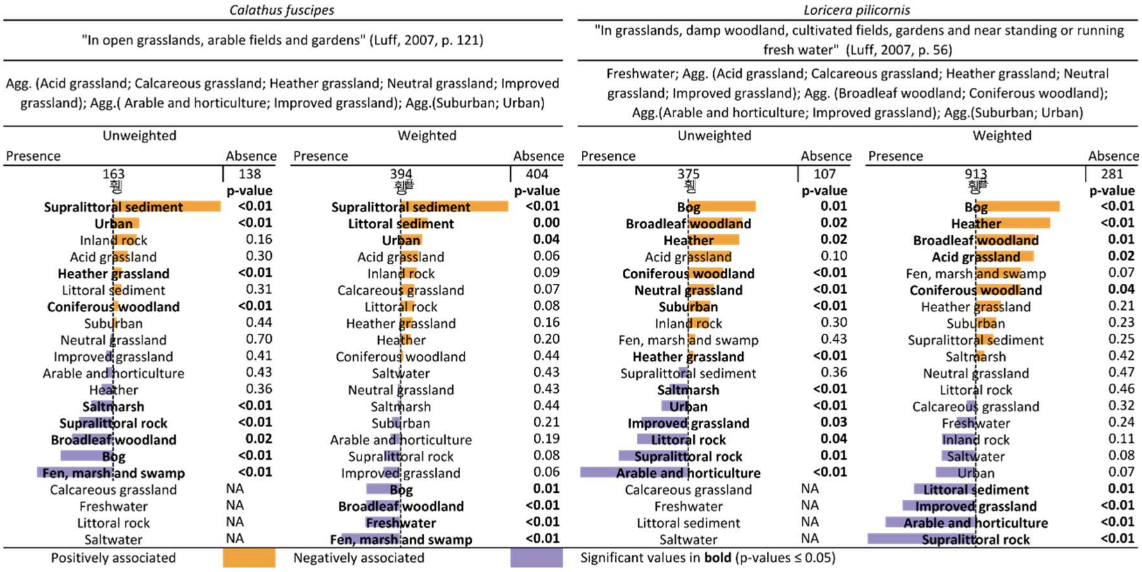
Freshwater

Unweighted: Presence 184	Absence 176 p-value	Weighted: Presence 449	Absence 444 p-value
Fen, marsh and swamp	**<0.01**	**Fen, marsh and swamp**	**<0.01**
Heather	**<0.01**	**Heather**	**<0.01**
Neutral grassland	**<0.01**	**Neutral grassland**	**<0.01**
Broadleaf woodland	0.10	Saltmarsh	0.07
Freshwater	0.07	Heather grassland	0.07
Saltmarsh	**<0.01**	Broadleaf woodland	0.16
Heather grassland	0.14	Bog	0.25
Littoral sediment	0.32	Freshwater	0.48
Coniferous woodland	**<0.01**	Coniferous woodland	0.49
Supralittoral rock	0.37	Littoral rock	0.39
Bog	0.47	Arable and horticulture	0.28
Suburban	0.49	Littoral sediment	0.24
Arable and horticulture	0.26	Inland rock	0.18
Acid grassland	0.26	Calcareous grassland	0.17
Urban	**<0.01**	**Saltwater**	**0.01**
Supralittoral sediment	**<0.01**	Acid grassland	0.08
Improved grassland	**<0.01**	**Suburban**	**0.04**
Calcareous grassland	NA	**Urban**	**0.02**
Inland rock	NA	**Supralittoral sediment**	**0.01**
Littoral rock	NA	**Supralittoral rock**	**0.01**
Saltwater	NA	**Improved grassland**	**<0.01**

Positively associated 🟧 Negatively associated 🟪 Significant values in **bold** (p-values ≤ 0.05)

Figure 2-2 Abax parallelepipedus and Acupalpus dubius original and weighted habitat correlation analysis showing the relative positive and negative ϕ and p values. These examples show the improvement offered using the weighted method, matching better with Luff and including more habitats.

Calathus fuscipes and *Loricera pilicornis* are two examples of species that matched Luff habitats better in the original than the weighted version, which failed to match open grassland and suburban respectively (Figure 2-3). For both species the named habitat remained positively associated in the weighted analysis, but had higher p-values, 0.16 and 0.23 respectively.



Calathus fuscipes

"In open grasslands, arable fields and gardens" (Luff, 2007, p. 121)

Agg. (Acid grassland; Calcareous grassland; Heather grassland; Neutral grassland; Improved grassland); Agg.(Arable and horticulture; Improved grassland); Agg.(Suburban; Urban)

Unweighted: Presence 163	Absence 138 p-value	Weighted: Presence 394	Absence 404 p-value
Supralittoral sediment	**<0.01**	**Supralittoral sediment**	**<0.01**
Urban	**<0.01**	**Littoral sediment**	**0.00**
Inland rock	0.16	**Urban**	**0.04**
Acid grassland	0.30	Acid grassland	0.06
Heather grassland	**<0.01**	Inland rock	0.09
Littoral sediment	0.31	Calcareous grassland	0.07
Coniferous woodland	**<0.01**	Littoral rock	0.08
Suburban	0.44	Heather grassland	0.16
Neutral grassland	0.70	Heather	0.20
Improved grassland	0.41	Coniferous woodland	0.44
Arable and horticulture	0.43	Saltwater	0.43
Heather	0.36	Neutral grassland	0.43
Saltmarsh	**<0.01**	Saltmarsh	0.44
Supralittoral rock	**<0.01**	Suburban	0.21
Broadleaf woodland	**0.02**	Arable and horticulture	0.19
Bog	**<0.01**	Supralittoral rock	0.08
Fen, marsh and swamp	**<0.01**	Improved grassland	0.06
Calcareous grassland	NA	**Bog**	**0.01**
Freshwater	NA	**Broadleaf woodland**	**<0.01**
Littoral rock	NA	**Freshwater**	**<0.01**
Saltwater	NA	**Fen, marsh and swamp**	**<0.01**

Loricera pilicornis

"In grasslands, damp woodland, cultivated fields, gardens and near standing or running fresh water" (Luff, 2007, p. 56)

Freshwater; Agg. (Acid grassland; Calcareous grassland; Heather grassland; Neutral grassland; Improved grassland); Agg. (Broadleaf woodland; Coniferous woodland); Agg.(Arable and horticulture; Improved grassland); Agg.(Suburban; Urban)

Unweighted: Presence 375	Absence 107 p-value	Weighted: Presence 913	Absence 281 p-value
Bog	**0.01**	**Bog**	**<0.01**
Broadleaf woodland	**0.02**	**Heather**	**<0.01**
Heather	**0.02**	**Broadleaf woodland**	**0.01**
Acid grassland	0.10	**Acid grassland**	**0.02**
Coniferous woodland	**<0.01**	Fen, marsh and swamp	0.07
Neutral grassland	**<0.01**	**Coniferous woodland**	**0.04**
Suburban	**<0.01**	Heather grassland	0.21
Inland rock	0.30	Suburban	0.23
Fen, marsh and swamp	0.43	Supralittoral sediment	0.25
Heather grassland	**<0.01**	Saltmarsh	0.42
Supralittoral sediment	0.36	Neutral grassland	0.47
Saltmarsh	**<0.01**	Littoral rock	0.46
Urban	**<0.01**	Calcareous grassland	0.32
Improved grassland	**0.03**	Freshwater	0.24
Littoral rock	**0.04**	Inland rock	0.11
Supralittoral rock	**0.01**	Saltwater	0.08
Arable and horticulture	**<0.01**	Urban	0.07
Calcareous grassland	NA	**Littoral sediment**	**0.01**
Freshwater	NA	**Improved grassland**	**<0.01**
Littoral sediment	NA	**Arable and horticulture**	**<0.01**
Saltwater	NA	**Supralittoral rock**	**<0.01**

Positively associated 🟧 Negatively associated 🟪 Significant values in **bold** (p-values ≤ 0.05)

Figure 2-3 Calathus fuscipes and Loricera pilicornis original and weighted habitat correlation analysis showing the relative positive and negative ϕ and p values. Showing that in these cases the original version matched more Luff habitats than the weighted version. The weighted method does however manage to represent more of the habitats.

2.4.2.2 Number of records required

Species with between 10 and 35 records in the weighted analysis gave matches with an average of 66% of Luff habitats. With so few presence records, however, the analysis had less power to differentiate habitats and to detect significance. For *Amara curta* the analyses was not able to detect any avoided habitats and analysis failed to pick up on the heath association suggested by Luff (2007). With 50 or 60 records, as in the case of *Bracteon litorale* or *Harpalus anxius*, the analysis was more able to differentiate the individual habitats. *Bracteon litorale,* which Luff (2007) describes as “On bare sand and fine shingle near rivers or standing water”, was associated in our analysis with broadleaved woodland and improved grassland, as well as agreeing with Luff by including freshwater. For *Harpalus anxius,* the analysis seemed to select the dunes of Luff’s description well, with supralittoral sediments the most preferred habitat, but did not select heaths. Additionally a positive association with saltmarsh was identified, which is often near dunes (Figure 2-4).

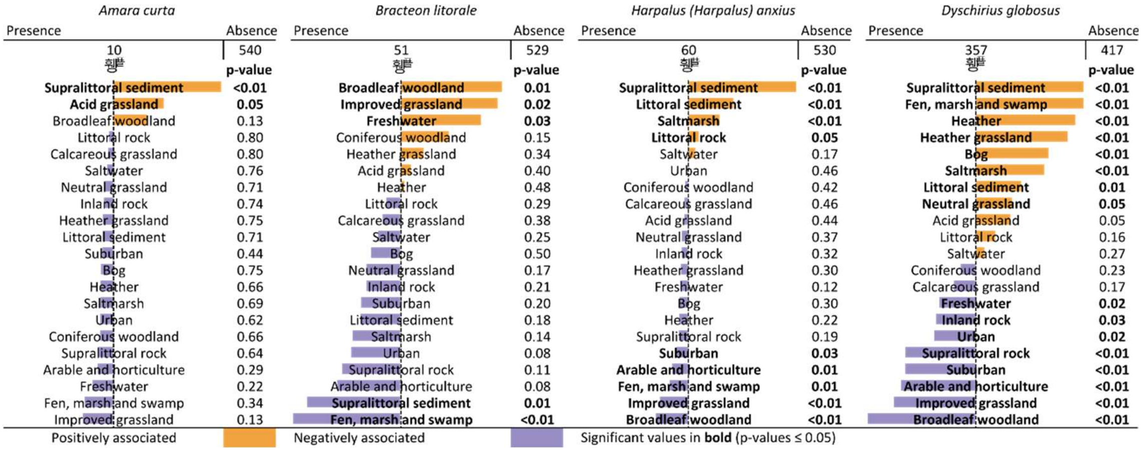


Figure 2-4 Amara curta, Bracteon litorale, Harpalus anxius, and Dyschirius globosus weighted habitat correlation analysis showing the relative positive and negative ϕ and p values. Showing that with more than 50 records the analysis gives both significantly positive and negative association.

2.4.3 Sensitivity analysis

Spearman’s rank correlation values were high when comparing habitat association calculated with the threshold value of 14 to a threshold of seven or 28 (Table 2-2). Even comparing the seven to the 28 threshold, the rank of the habitats remained consistent.

Table 2-2 Comparison of the habitat associations using Spearman’s rank correlation between different thresholds of species numbers used to define absence squares in the analysis of carabid land cover association.

	Threshold 7 and 14	**Threshold 14 and 28**	**Threshold 7 and 28**	**Number of species**
Original	0.90 (SE 0.004)	0.86 (SE 0.009)	0.80 (SE 0.011)	212
Weighted	0.95 (SE 0.002)	0.89 (SE 0.007)	0.84 (SE 0.009)	268

2.5 Discussion

Our new weighted version of the Phi correlation index allowed substantially more records to be included for each species and therefore increased the number of species that could be analysed and improved the predictions of habitat association. The use of the number of species records as a proxy of survey effort was robust, being insensitive to the threshold for defining absence locations. The weighted analysis was able to give accurate results with as few as 50 records, and the use of absences enhanced the ability to determine habitat associations. Informative results using so few records are in stark contrast to other methods which require thousands of records for each species. Redhead et al. (Redhead et al., 2016) suggest that few taxa are well-enough recorded to provide so many records, our improved method will be applicable to many more taxa. For example, 35% of cerambycid beetles have 50 or more records in Great Britain (44% for carabids). Our method also gives a target for recording the rarer specialist species, whose conservation most requires an evidence base (Lawton et al., 2010).

As the number of records gets very large the Phi coefficient becomes the Ochiai index, which is itself related to a modified version of IndVal (De Cáceres et al., 2008). The number of records in the data we have are not large and the Ochiai index was therefore not applicable. It is possible, however, to extend both the non-equalized and group-equalised IndVal in a similar way to the phi coefficient we present in this paper by adding habitat weighting. The values still range between zero and one and the weighted version gives a value for more of the habitats. The results of weighting IndVal have not been tested, but this could be done in future research identifying indicator species. To facilitate such a test, this capability is included in our PhiCor R package. Dufrêne and Legendre (Dufrêne and Legendre, 1997) used carabid data from pitfall traps to validate IndVal originally. The capture locations of all individuals were known precisely. However, besides using the weighting for imprecise locations, as presented in our case study on the phi coefficient, the weighting method could be useful in cases with precise locations for a number of the indices presented in De Cáceres and Legendre (2009). These cases include species foraging or dispersing into neighbouring habitats (McIntire et al., 2013), source-sink dynamics of plants (Kadmon and Shmida, 1990), or to account for the uncertainty of land cover classification (Morton et al., 2011). It may even be worthwhile drawing buffers around record locations so as to include information on surrounding habitat.

Unlike species distribution models, the correlation index does not suffer from overfitting (Breiner et al., 2015). However, as numbers of presences and absences differ between species, comparison among species is not straightforward. The maximum ϕ values vary with the number of records and are rarely comparable between species. The rank of the habitats is comparable but where two species have similar ranks for a habitat they may not have the same affinity. The number of positive habitats for each species, however, is positively correlated with the degree to which a species is categorised independently as generalist *vs* specialist (see Appendix C2.6).

One possible way of increasing the comparability between species is to use the group equalised correlation index (Tichy and Chytry, 2006). Beyer et al. (2010) reviewed the factors influencing habitat preference of species, arguing that species which are found more often are so because the habitat is more common. Tichy & Chytry (2006) suggested a group (habitat) equalised version of the correlation index. This version modifies several of the inputs by the number of groups. In our case, group equalising usually resulted in the same habitats having significant associations, although the ϕ values were often different. As an example, *Bembidion lampros* is associated in the non-equalised analysis with arable followed by conifer and urban. In the equalised analysis the same habitats are retained in the top three, but now the beetle is most associated with coniferous, urban and then arable. A weighted group-equalised version (Appendix C2.7) did not match the Luff (2007) validation data quite as well, but is included in the full output (Appendix C2.5). It should be noted that species may not be equally detectable in different habitats and therefore, where the data is available a similar equalisation could be done using detectability.

The analysis we have conducted agrees to some extent with previous smaller scale studies of carabids using different analytical approaches. Eyre and Luff (2004) used constrained ordination with 126 carabid species against the proportion of 12 habitats within 1 km squares across north-east England and south-east Scotland. Some of their results agree with ours, although, as an example, their analysis suggests a higher preference of *Abax parallelepipedus* for inland water than broadleaved woodland. Eyre and Luff (2004) point out that some unexpected relationships of species and land covers suggest care is needed when interpreting their results and that the low eigenvalues and cumulative percentage variation suggest noisy data.

Within the literature the same species is sometimes attributed to different habitats in different studies without clear information on where this association information stems from or the species' other associations. An example is *Pterostichus madidus,* which is variously described as inhabiting dry open, urban, moorland or grassland (Butterfield et al., 1995; Dennis et al., 2004; Angold et al., 2006; Morecroft et al., 2009), with Luff (2007) describing the species as "woodland, garden and dry grassland". Our analysis agrees with all of these habitats, suggesting the species is associated with a wide range of habitats. The method we present provides a robust method of presenting all the associations of a species, which can be used to paint a clearer picture of habitat associations.

We chose in the main analysis to remove record locations with more than one habitat. Another option was to choose the most abundant habitat. We conducted a version of the unweighted analysis choosing the most abundant habitat in each 100 m square. This version matched the Luff (2007) validation less well than the unweighted version removing records (Appendix C2.2). This is likely due to misclassification of the habitat that the species was found in or the loss of information about which habitat individuals of the species could have been in prior to being caught.

In conclusion, our new weighted method demonstrates an improvement to the Phi coefficient of association, which is simpler than ordination, requires fewer records than regression, and gives habitat preference and avoidance. Our method allows for uncertainty in the habitats associated with the record location and is ideal for mobile species, which may be found outside of preferred habitats. It utilises more of existing sources of data, including every habitat within a non-point location, giving quantitative information on habitat preference. Our work provides guidance on the flexible threshold defining absence records and targets for the number of records necessary to achieve a reasonable result for each species. The method is usable as-is to provide detailed data usable in conservation planning and the case study provides the carabid analysis ready to use in modelling and improving interpretation of the results of future studies. Having established the method as working for carabids, the method would benefit from further testing with different taxa.

2.6 Data Accessibility

CEH LCM2015 (Rowland et al., 2017a) is available for academic purposes from https://doi.org/10.5285/6c6c9203-7333-4d96-88ab-78925e7a4e73. National Biodiversity Network (NBN) atlas (2017) carabid data is available from https://species.nbnatlas.org/species/NHMSYS0001717497.

Chapter 3

Individual-based model, Overview, Design concepts and Details

3.1 Introduction

The remaining data chapters of this thesis look at *fragmentation per se* (FPS), and investigate if differences in species and habitat matrix between FPS patches may alter the relationship of alpha-, beta-, and gamma-diversity to FPS. Due to the difficulties in conducting this sort of analysis in the field in terms of time, money, and availability of sites and the difficulty of looking at fragmentation while controlling for the area, I chose to look at FPS by using a modelling approach, by using an *individual-based model* (IBM). I used an IBM in a multi-species and landscapes simulation to allow me to look at the emergent properties of having multiple individuals and species moving around a landscape containing a high number of patches and habitats. Other options than IBM for looking at the effect of a large number of patches with species having multiple preferences would have been difficult if not computationally and mathematically impossible. Deterministic models would struggle to with the large numbers of patches and the complexity of multiple land-covers in the matrix between a fragmented land cover (Kanagaraj et al., 2013), traditional modelling approaches also fail to capture variability caused by individuals (Railsback and Grimm, 2017).

Our simulation had much in common with other IBMs, density-dependence at a cell scale, random distance of movement up to a maximum distance and random starting locations (Fahrig, 2001).Other IBMs have used multiple species (Shin and Cury, 2004) and studies have looked fragmentation (May et al., 2019) or connectivity (Hunter-Ayad and Hassall, 2020), few other models look at fragmentation using multiple species, and then only in part of the landscape (Rybicki et al., 2019). My simulation looking at fragmentation contains multiple generic species within each simulation run and in not being limited to using a binary landscape of focal-habitat and matrix, allowing different species to have different land cover associations within a single landscape (Nabe-Nielsen et al., 2010; Betts et al., 2014; Chetcuti et al., 2019). I focus on generic species in the hope of finding generalisable results and not results only specific to a small number of species or a genus. FPS is defined and mitigated at a human perspective that may not match a species perspective (Bollmann et al., 2005; Betts et al., 2014; Brodie and Newmark, 2019; Chetcuti et al., 2019). My approach continues to classify the fragmented habitat from the perspective of a human classified land cover while utilising a benefit of IBM and allowing species level perspectives with species having different associations with the focal-habitat and matrix land covers. Having increased the complexity of the simulation with multiple species and land covers, I kept the individual species simplistic. The simulation does not contain seasonality and the associated difference in when species reproduced, nor did it include different dispersal and foraging movement behaviour. I instead opted to focus the simulation instead on the interaction of species with the landscape and how these species move in an attempt to see if, even with these simplistic species it was possible to show differing effects of FPS. My IBM was built and run in NetLogo (v6.0.4) software (Wilensky, 1999). No random seed was set instead automatically set for each simulation run by the system time. The random numbers were then generated using a Mersenne Twister (Wilensky, 1999). The model description follows the ODD (***O**verview, **D**esign concepts, **D**etails*) protocol for describing individual- and agent-based models (Grimm et al., 2006; Grimm et al., 2010).

3.2 Overview

3.2.1 Purpose

The purpose of this IBM is to allow for the simulation of the interactions of multiple species with landscapes and record the habitat and patch at the end of the simulation. This sort of simulation is necessary to go beyond single species, binary, few patch deterministic models and to allow for the creation and interaction of multiple species with multiple habitats within a landscape. This sort of simulation is also interesting as it allows the exploration of different walk types for the species. In this simulation, three walks can be set; random walk (RW), correlated random walk (CRW) and a habitat dependent walk (HDW). Initially, this simulation will be used in three studies, but the hope is that this simulation could be used to answer many different questions going into the future. The outputs of these simulations can be used to look at changes in abundance and diversity (alpha, beta, gamma and zeta) of different species or types of species. The outputs can also be used to look at the full movement path of individuals within the simulation. The user of the simulation can either, define abstract species or, to a degree, real-world species

3.2.2 Entities, state variables, and scales

The entities in this IBM are not based explicitly on any real species or sets of species but can be parameterized to represent real species. Each entity type or species is defined primarily by its habitat suitability, representing both suitability and preference of species to the habitats (a ranking of all possible habitats) and optionally secondarily by the degree to which this suitability influences bias in choosing habitat, reproductive probability, mortality probability and how the species walks in different habitats. Species can have different speeds, maximum reproductive rates, inter and intra-species density-dependent mortality, walks and starting numbers.

Each individual has a set of variables, with only some of them changing every turn:

These change in every turn:

- Heading – the direction the individual is facing.
- X-coordinate – the location on the x axis of the individual.
- Y-coordinate– the location on the y axis of the individual.

These are different for offspring:

- Individual ID – every individual has a unique integer that identifies the individual.

Unchanging variables that are stored and inherited for each individual.

- Species ID – the different species also have an ID shared by all individuals of that species.
- Walk information
    - Walk type – RW, CRW, HDW – species can move with different walks, random, correlated and habitat dependent walks.
    - HDW exponent – the HDW walk is defined by a negative exponential function. This is the exponent and determines how quickly the walk becomes more directed with progressively less suitable land cover.
    - multiplier to the CRW angles
- Speed or maximum movement distance – the furthest and individual can move in a single time step. The emergent movement behavior of this approach will be a dispersal kernel with more individuals moving shorter than the maximum and few at the maximum.
- Maximum reproductive rate – the probability of an individual having an offspring within a single time step.
- Intra and inter species density – how many individuals can survive in the same cell.
- Habitat bias slope – the slope of the logistic equation that defines how strongly biased species are towards choosing preferred habitat.
- A habitat mortality slope– the slope of the logistic equation that defines how strongly the additional mortality increases in less suitable land cover.

- A habitat reproduction slope– the slope of the logistic equation that defines how strongly the reproduction decreases in less suitable land cover.

The following variables are lists giving a value for each habitat calculated using the HDW exponent, habitat bias slope and mortality slope respectively. These values are set for the species and do not change, they are calculated at the beginning and stored. Doing so makes the simulation run faster as it requires fewer calculations.

- Habitat field of view (these are only used for the HDW)
- Habitat Bias multiplier
- Habitat mortality multiplier
- Habitat reproduction multiplier

For all of the variables used by the individuals within the simulation, users of the simulation can either define that a variable is the same or different for each species. If the values are different, they are loaded from tables. The tables have a row for each species. The rows in the different tables relate to the same species.

The habitat bias and mortality slope multipliers between zero and one and are each given by the slope of a negative logistic relationship that calculated the multiplier from the habitat suitability rank. These multiplier values are less than one, reducing the probability of moving to a cell or the reproductive rate to be lower in less preferred habitat. So that the additional habitat dependent mortality is of a similar order of magnitude to the rate of reproduction, the habitat mortality multiplier multiplies by the same number as used in the rate of reproduction. This then gives an additional mortality between close to zero in suitable land cover and almost equaling the reproduction in the least suitable land cover (in most cases, although this can be defined to be lower in least suitable land cover).

The individuals can be set to either move using an RW, CRW or HDW. The HDW moves like an RW or CRW depending on the habitat. When moving using the RW the individuals observe the cells around it and randomly up to a distance defined by the speed. The habitats are assigned a probability of being selected based on $p_n \left(1 - 1/\left(1 + e^{-x(\varphi_n - 11)}\right)\right)$ where p_n is the proportion of the circle that is habitat n and φ_n is the habitat preference for habitat n and x is the slope of the logistic equation. In retrospect I should have, for the CRW walk, used a wrapped Cauchy distribution with mean of zero and a concentration parameter (p) which would allow us to specify an uncorrelated walk (p=0) to a perfectly correlated walk (p=1). However, we used a gamma distribution (alpha = 1, lambda = 2) multiplied by 360°. We then made it more or less correlated by multiplying values. When the value exceeded 360° we redrew the number from the distribution. The HDW uses a negative exponential equation to determine the range of angle the individual can choose from when walking. In preferred habitat, the walk is, therefore, an RW and then becomes progressively more correlated.

The simulation has no inherent spatial or temporal scale. These can be defined using data on the species or genera of interest or by using approximations from allometric equations. So, for example, if a species group of interest moved between 2 and 20 km h^{-1} then, it would make sense for a cell to be a kilometer and the time step to be an hour as then individuals could be set to move between two and twenty cells per time step. We use the simulation with a vertical and horizontal extent of either 1000 or 1020 cells (depending on if we have a buffer or not). Changing the extent from the current one 1000-1020 would require a new version, as the extent is assumed to be 1000-1020 during the setup procedure.

The landscapes are loaded from two ascii files, one containing the land cover which should match the possible suitabilities in the setup for the species (although not all habitats need to be present) and the other defining the habitat patches.

3.2.3 Process overview and scheduling

The time is modelled as discrete time steps.

In each time step:

1. All individuals are cycled through in random order.
    a. Die if a uniform random draw is less than habitat-based mortality (if the simulation has this setting turned on).
    b. Reproduce if a uniform random draw is less than the maximum reproduction (multiplied by habitat-based reproduction if this is turned on).
    c. To count the number of individuals in a radius of their self and if higher than the threshold to die (inter and intra-species density).
    d. If the whole population of the simulation is over a carrying capacity, then the individuals draw a random number against the proportion over the carrying capacity and die if the random number is below the proportion.
    e. To assess its surroundings and move (see 2.3 Entities, state variables, and scales)
2. Finally, the time is moved forward one step.

All random numbers used above are between zero and one. Reproducing individuals spawn an individual at its location sharing all variables but setting a new individual ID and the heading randomly.

The simulation is perceptually toroidal to allow the circle or sector of the individuals to be complete and not interfere with the movement of individuals, but individuals can be stopped from moving across the boundary by having individuals die if they do cross over (this can be turned on or off). So that the habitat on the other edge of the landscape does not influence the individuals, causing them to pass over the edge of the simulation more or less probably, a 10-cell random habitat edge buffer can be included. The random land cover edge can be turned off, for example, if the land cover used is simplistic, with the same habitat along all edges, then the random edge is not necessary.

3.3 Design concepts

3.3.1 Emergence

The simulation can use several different modes to output results.

- SinglespeciesLocation and MultispeciesLocation –these report functions can be used for a single individual or multiple, to record in every time step:
    - Individual ID
    - Species ID
    - Current location
        - Land cover
        - Patch ID
        - X
        - Y
- count turtles - the NetLogo default, to count the overall population either every time step or at the end of the simulation
- species-count – is the number of species. Can report either every time step or at the end of the simulation.
- saveOutPitfall and saveOut – these two reporter functions output two csv files, turtle and patches. The turtle csv file contains three unlabeled columns, which correspond to species id, land cover class and patch ID. The patches csv contain two unlabeled columns, land cover class and patch ID. The pitfall function records the individuals that cross the approximate central cell of a patch for a defined period before the simulation end and outputs the files. The non-pitfall version records every individual at any location. These two functions can both be used together at the end of a simulation. If a habitat of interest is defined (HabInterest), then the pitfalls are only set up in this habitat and for both output types the species are only recorded in the focal-habitat.

Reproductive and mortality rates overall and in each habitat, the patterns of land covers and species suitability and the way the individuals move will influence the number of individuals and their distribution within each simulation.

3.3.2 Adaptation

The individuals in the simulation randomly select where to move to within a circle or sector of a circle. This random choice can be biased by preference. Density-based mortality is based on individual observation of the cell they are in or those in an area around them. The order the individuals are cycled through is random, therefore an individual dies if it observes there are too many individuals in its vicinity.

3.3.3 Fitness

Fitness is not usually sought. Increasing bias towards preferred habitat when habitat-based reproduction and or mortality is implemented could be considered seeking out habitat that optimizes fitness, but there is still a lot of randomness. They also can only perceive up to the maximum distance they can move in a time step and they have no memory for where they have been.

3.3.4 Predictions

Individuals do not predict future conditions.

3.3.5 Sensing

Individuals are aware of the habitat they are in, how many other individuals are in the same cell or the surrounding cells (intrRadius and interRadius ≥ 0). They are aware of the cells up to the maximum distance they can move within either a circle or a sector depending on the walk.

3.3.6 Interaction

Individuals only interact with one another via density-dependent mortality. If there are more individuals in their cell than specified, then the individual counting dies. The species are cycled through in a different order every time. When an individual dies, it is immediately removed. This means that if the density dependence was set as a maximum of two individuals in a cell, then if a cell contained five individuals, the first three polled would die, but the fourth and fifth would live.

3.3.7 Stochasticity

- If the random edge is turned on then the cells in this zone are randomly assigned habitat, this is to avoid influencing individuals with the habitat on the other side of the simulation, but still let the circle or sector of a circle include cell across the edge of the simulation. This makes them leave the simulation randomly.
- Individuals start at a random location.
- New individuals have a random heading assigned.
- When the walk is set to CRW an angle is selected from a random gamma distribution and is used to define the sector of a circle the individual observes and can move into.

- The maximum distance the individual observes and can move into is randomly selected up to the maximum speed for the species.
- A random number between zero and one is used to decide which habitat to move to weighted by bias and proportion. A cell within this habitat is then randomly chosen.
- Random fractions are compared to the carrying capacity mortality and habitat mortality for each individual meaning that on average the mortality is a combination of each of these sources of mortality.
- A random fraction compared to the reproduction rate adjusted by habitat.

3.3.8 Collective

Individuals are assigned and inherit a species ID but do not act as a collective.

3.3.9 Observation

If the user is using the simulation with the graphic user interface, they can see the land cover and different colour individuals, coloured by species. This allows species clumping and movement to be observed. Sometimes it is useful to ask turtles to set their pens down as you can then see where individuals have been. A graph of the population and number of species can be seen on the right. The population graph can be set to show the numbers of each species.

3.4 Details

3.4.1 Initialization

The simulation does not have a single set of initialization values.

3.4.2 Input data

The model does not use input data to represent time-varying processes. Land cover data is loaded for each simulation. The values are specified for the experimental scenarios. Many of these values are kept constant in the current study, but could be changed.

3.4.3 Submodels

Individuals having different habitat suitabilities is based on the work in Chapter 2 on habitat association of carabids using the Phi coefficient of association (De Cáceres and Legendre, 2009). This work gave a value between one and negative one defining the positive and negative association of the habitat to the species. At this stage, we do not know to what extent this association is driven by the choices of the individuals or reproductive success and mortality of the species within each habitat. The relationship between the ranked habitat association and the associated value is similar to a sideways s-shape. For simplicity, I decided therefore to use a negative logistic equation to relate the ranked association of each species to the bias towards preferred habitat, habitat growth rate, and mortality. The values calculated for each habitat are used as a multiplier to the probability of choosing a habitat or reproduction and mortality values for individuals of an individual while it is in that habitat. The multiplying values are between zero and one (equation (3-1). To calculate the habitat bias of habitat, the proportion of the circle or sector that is each habitat is calculated and then the proportion of the area that is each habitat is multiplied by the multiplier value these are then normalized and cumulatively summed. A single random number can then be used to select the habitat using the cumulative sum value for each habitat.

The habitat reproductive rate is calculated by multiplying the mean reproductive rate multiplier values and habitat mortality by multiplying the mean reproductive rate by one minus the multiplier.

$$Multiplier_n = \frac{2}{1 + e^{x(\varphi_n - 11)}} \tag{3-1}$$

Where x is the slope value assigned for the habitat bias, reproduction or mortality and n is the habitat and φ_n is the habitat suitability rank. The midpoint of the negative logistic equation can be set based on the number of habitats, for example, we set it as 6 as we have 11 habitats. Another advantage to using a logistic equation is that on average over all of the habitats, if they all had equal proportions in the landscape, the total bias, reproduction or mortality would be the same regardless of the slope that was used.

Chapter 4

Fragmentation increases diversity, but not of species that depend on the habitat

4.1 Abstract

Debate rages as to whether habitat fragmentation leads to the decline of biodiversity once habitat loss is accounted for. Previous studies have defined fragmentation variously, but research needs to address "fragmentation per se", which excludes confounding effects of habitat loss.

I have defined fragmentation per se of a focal-habitat with a species level perspective of the rest of the landscape. Using a multi-habitat, landscape-scale, individual-based model that incorporates movement, I investigated how fragmentation per se changes diversity and if this differs among species groups according to their habitat dependency and specialism. I defined specialism as increased competitive ability of specialists in suitable land cover, and decreased ability in less suitable land cover compared to generalist species.

I found fragmentation per se caused an increase in gamma-diversity of all species in the focal-habitat. But, critically for conservation, the gamma-diversity of species for whom the focal-habitat is most suitable, declined under fragmentation per se. My specialist species were unaffected by fragmentation per se. My findings help to inform the fragmentation per se debate, showing effects on biodiversity can be negative or positive, depending on species' competitive ability and dependency on the fragmented habitat. My study employs a mechanistic multi-species model to identify mechanisms that cause some species to be more or less sensitive to fragmentation per se.

4.2 Introduction

Humans have modified over 75% of the global land area, and the resulting habitat loss and degradation is recognised as the principal driver of biodiversity declines (IPBES, 2018). A major consequence of landscape modification is that in many locations, previously large blocks of natural habitats have become fragmented into small patches in a matrix of human-modified land-use such as farms and cities (Haddad et al., 2015). It is clear that habitat loss reduces species diversity, simply by shrinking the areas in which species using that habitat can live (MacArthur and Wilson, 1967; Hodgson, Moilanen, et al., 2011; Keil et al., 2015). However, the effect of fragmenting habitats is less clear. “Fragmentation per se” (FPS) refers to the effects of fragmentation after taking account of, or in the absence of, habitat loss (Fahrig, 2003). Put another way, it comprises the altered spatial configuration of habitat with no habitat loss, such that remaining patches are smaller but more numerous. In reality, fragmentation and loss of habitat are intrinsically linked (Fletcher et al., 2018). Nonetheless, separating the effects of FPS from those of area loss and defining under what circumstances FPS leads to higher or lower species diversity are important for conservation decisions, such as restoration of habitat networks (Isaac et al., 2018). The consensus in the conservation literature has been that fragmentation in general is detrimental to biodiversity (Lawton et al., 2010; Eigenbrod et al., 2017). Considering FPS specifically, debate continues as to whether the effect of FPS on biodiversity is generally negative (Fletcher et al., 2018), insignificant or positive (Fahrig, 2017; Fahrig et al., 2019). Understanding how positive *vs* negative effects of FPS on diversity may arise according to species’ characteristics such as specialisms and habitat associations, will aid decisions about how to manage specific landscapes. Decisions include whether to conserve multiple small or fewer large habitat patches (Tulloch et al., 2016) or to allow activities that may lead to a limited loss of habitat, but fragmentation (Miller-Rushing et al., 2019).

It is often assumed that specialist species and those that are positively associated with the focal-habitat should be negatively affected by FPS (Kosydar et al., 2014; Halstead et al., 2019). If studies report a positive effect of FPS, one explanation given is that species richness and abundance of generalists increases with habitat fragmentation, leading to this rise in diversity (Hu et al., 2012). But in 97% of the studies considered in a review by Fahrig (2017), FPS had a positive effect on the landscape-level diversity of specialist, rare, or threatened species. This could be because FPS allows for separation of otherwise competing species among patches of the focal-habitat within the landscape (Ramiadantsoa et al., 2018). Specialist and generalists are often defined by an association with a particular land-cover or with many respectively, but this association is open to interpretation (Da Silveira et al., 2016). Being a generalist does not mean the species does not have habitat preference (Townsend et al., 2008; Da Silveira et al., 2016). Chetcuti et al. (2019) looked at the habitat association of hundreds of species, showing most species had a positive association with a number of land covers, and only a few species showed a strong restriction to only two or three land covers. Specialists have also been defined as being more competitive in a preferred or more suitable land cover compared to a competitively inferior generalist in that land cover, but the generalist more competitive in general across multiple land covers (Marvier et al., 2004). Here I define specialists as being more competitive in suitable land cover than generalists are, but less competitive than the generalists elsewhere, even where the species may share the same habitat preferences within a landscape.

Long-term manipulation experiments show that patch attributes typically associated with fragmentation (e.g. reduced patch size), reduce biodiversity at the scale of an individual patch, i.e. alpha-diversity (Haddad et al., 2015; Fletcher et al., 2018; Damschen et al., 2019). However, it has been suggested that mechanisms identified in patch-scale studies may not extrapolate to negative effects on biodiversity at the landscape scale (Fahrig, 2017). Indeed, at the landscape scale, across multiple patches of that focal-habitat, Fahrig (2017) reports that different studies report either a neutral or a positive response of biodiversity (gamma-diversity) to FPS (Fahrig, 2017). By contrast, the species-fragmented area relationship suggests that negative effects of FPS should reduce gamma-diversity from that predicted by the species-area relationship (Hanski et al., 2013). However, the modelling behind species-fragmented area relationship and patch scale studies do not take into consideration mechanisms that lead to potential positive effects of fragmentation, such as increased beta-diversity caused by competitive release and higher land cover diversity (Fahrig et al., 2019; Rybicki et al., 2019). These mechanisms may increase beta-diversity and lead to overall increase in gamma-diversity with FPS.

At the patch scale, there is also another problem. It can be difficult to separate the effects of loss of area from those of FPS, as highly fragmented habitats are often in smaller patches (Fahrig, 2003). Controlling area is not only a problem for patch-scale studies. In general conduction manipulative landscape-scale studies are difficult and it is often impossible to control for habitat area, which results in a confounding of FPS with habitat loss (Fahrig, 2003; Betts et al., 2019). The effects of area can be isolated statistically (Fahrig, 2017; De Camargo et al., 2018), but in these cases, the change in area can swamp any FPS signal (Fahrig, 2003). Theoretical modelling is a useful way to address contested issues where field data are difficult to collect and subject to confounding variables. To this end, simulation models have been used to study FPS, which allow individual organisms to move across simulated landscapes (Gunton et al., 2017; Rybicki et al., 2019). However, these studies, as with many other studies (Thompson et al., 2019), with few exceptions (Wiegand et al., 1999; Heinrichs et al., 2016), are conducted on binary landscapes with the space between the focal-habitat patches, the matrix, being a single land cover type. Obviously, binary landscapes are rarely found in nature, and so using a binary land cover likely reduces the relevance and applicability of these simulation studies (Fardila et al., 2017). With only a single matrix land cover, one possible mechanism of benefit of FPS is lost, that of increased land cover diversity. With FPS, patches of focal-habitat are adjacent to different matrix land covers, which can lead to higher diversity in the focal-habitat by providing a secondary habitat (Fahrig et al., 2019; Rybicki et al., 2019). By having multiple matrix land covers, edge effects, which are typically considered a negative mechanism of FPS, can have a positive effect (Fahrig et al., 2019; Betts et al., 2019). In this study, I modelled FPS in terms of a single land cover type. However, I used multiple matrix land covers, allowing for species level perspectives with each species having a different set of habitat preferences, thus better reflecting species' differences in nature (Bollmann et al., 2005; Betts et al., 2014; Brodie and Newmark, 2019; Chetcuti et al., 2019).

In this study, I use an individual based model (IBM) to provide a mechanistic assessment of FPS effects on alpha-, beta- and gamma-diversity, by simulating FPS at the landscape scale, with multiple matrix land covers, and for species with differing specialisms for, and dependencies on, the different habitats in the landscape. I predict that FPS will cause beta-diversity to increase because FPS allows the persistence of more species among different focal-habitat patches. Furthermore, FPS will increase the edge-to-area ratio and so the degree to which the focal-habitat interfaces with other land covers. This will lead to higher beta-diversity of species for whom the focal-habitat has high suitability due to species having access to a greater variety of secondary habitat, reflecting the different species-specific habitat preferences. This increased edge will also lead to an influx of species for whom the focal-habitat is less suitable. These tourist species, also called vagrant species (Magurran, 2004; Rickert et al., 2012), could potentially counter some of the overall loss in alpha-diversity, but lead to higher competition for species dependent on focal-habitat. Due to the well-known species-area relationship – that the relationship of increased sampling area to richness is positive – by leading to smaller patches, FPS will have a negative effect on alpha-diversity. Therefore, I hypothesize that, **1) Increasing fragmentation (FPS) of a habitat causes steeper declines in alpha-diversity due to increased competition from an influx of "tourist" species from the matrix, and therefore the gamma-diversity will decrease with FPS.** Focal-habitat dependent specialist species, which are more competitive in the focal-habitat they find most suitable, will be better able to hold out against the influx of tourist species. Generalists will be able to utilise more of the landscape and will coexist with the specialists, but will decline with fragmentation. Therefore I hypothesize that, **2) Declines in alpha-diversity with fragmentation of a habitat (FPS) will be less steep where the species using that habitat divide into specialists and generalists, due to decreased competition, and so gamma-diversity will be either unaffected or increase with FPS.** Additionally, I assess whether results are consistent at high (40%) *vs* low (10%) levels of focal-habitat cover, testing the fragmentation threshold hypothesis that FPS should only have a negative effect when habitat amount is low (Fahrig, 2017; De Camargo et al., 2018). I include some of the possible mechanisms of FPS, reduced competition, and higher habitat diversity. I also partially include edge effects, through the inherent increase in edge with fragmentation, but did not include edge micro-climate effects.

4.3 Methods

I created a multi-species and landscapes IBM simulation to look at the emergent properties arising from multiple individuals and species moving around a landscape containing a high number of patches and habitats (Figure. 4-1). My IBM was built using NetLogo (v6.0.4) (Wilensky, 1999). The simulation parameters were set up, run and the outputs analysed using R version 3.5 (R Core Team, 2018).

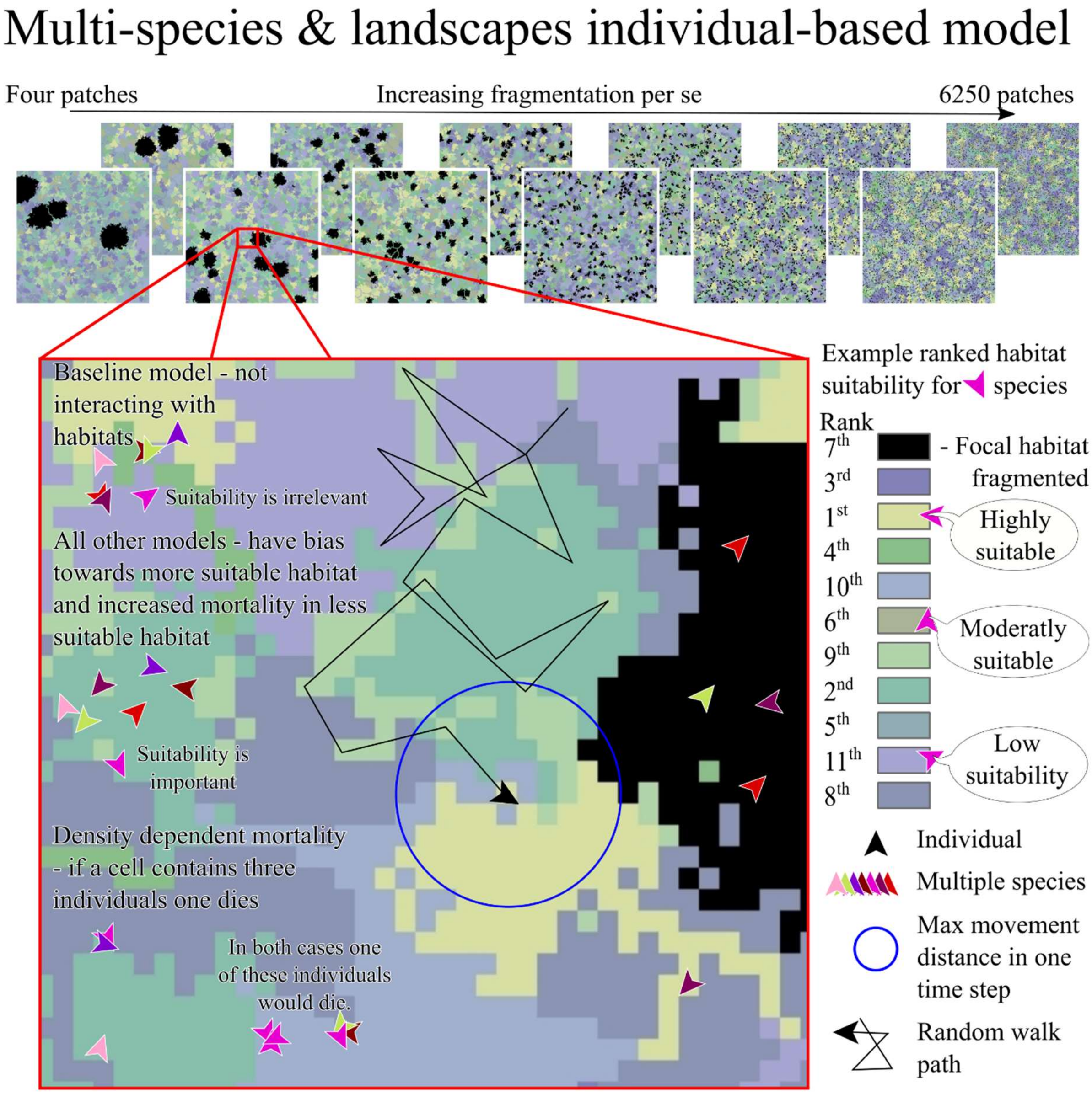


Figure 4-1 A figurative description of the individual-based model, showing how I represented FPS by increasing the number of patches of the focal-habitat (in black) while keeping its total area the same. I give an example of the ranked suitability for land covers on the right for one species and an example of a random walk in the middle. The simulation used a baseline model, in which the individuals did not have differing mortality or movement bias for different land covers. I simulated two other scenarios in which the individuals interact with the land covers according to their assigned suitability. In the first scenario, the habitat modified mortality and individuals showed biased movement. The second scenario was the same, with the addition that half of the species were specialists and half generalists. I defined specialists and generalists as the former being more competitive in preferred land covers and less competitive in non-preferred land covers compared to generalists.

I described the model in Chapter 3 following the Overview, Design concepts, Details (ODD), protocol for describing individual-based models (Grimm et al., 2006; Grimm et al., 2010), but summarise it here. Each scenario and FPS number of patches was repeated 50 times. Seventy-one runs failed due to java issues on the clusters leading to the minimum number of replicates being 45.

4.3.1 Land cover generation

I generated fragmented landscapes by increasing the number of patches of the focal-habitat while keeping area of focal-habitat constant. I generated land cover data to allow for exploration of FPS without confounding variables such as area loss that is often present in real data. I did this by writing an R script (supplementary material S2). The generated land covers contained patches that were a range of shapes (Figure 4-1). I generated land covers with eleven land covers: focal-habitat, and ten other land covers filling the matrix space. I defined the land covers from a human perspective, as in other fragmentation studies (e.g. Betts et al 2019). In keeping with the known complexity of species habitat associations, I allowed species to have a diversity of associations with and use of land covers within the landscape (Betts et al., 2014; Chetcuti et al., 2019). I generated a new landscape for every model run. Generating land covers of 1000 x 1000 cells was computationally intensive, so I generated at 250 × 250 cells and spatially resampled to 1000 × 1000 cells by making each of the 250 × 250 landscape cells four cells in the new 1000 × 1000 cells landscape.

I increased the number of patches of the focal-habitat geometrically starting with four patches (allowing beta-diversity calculation), up to a maximum number of patches. Patches of the same land cover were spatially separated by at least a cell for the 250 × 250 cells landscape (resulting in two cells at 1000 × 1000 cells). The maximum number of patches was defined as when each separate patch was one cell at 250 × 250 cells (four at 1000 × 1000 cells). For the 10% scenarios, this was 6250 patches. For the 40% scenario, I used a maximum patch number of 8192, less than the theoretical maximum, but computationally feasible. For the focal-habitat, I defined number of patches and percentage habitat cover. The patches were located in the landscape by generating random coordinates for starting locations using the r package ‘mobsim’(May, 2017). The program repeatedly chose a patch using a uniform random weighting. This allowed for a range of sizes not distributed around a certain size of patch. Patches grew by one cell until the area of the focal-habitat reached the required amount (10% or 40% of the total cells in the land cover). The program repeated the procedure for land covers two to eleven (in a random order) one at a time to fill remaining space. Each matrix land cover had between one and 200 patches and each covered a random proportion of the matrix. If any land cover was unable to grow any of its patches, then that land cover was considered complete and the next land cover grown. The last land cover filled all remaining space.

4.3.2 Multi-species landscape model description

My simulation had much in common with other IBMs, such as random-walking species, density-dependence at a cell scale, random distance of movement up to a maximum distance and random starting locations (Fahrig, 2001). My simulation differed in having multiple generic simulated species within each simulation run and in not using a binary landscape of focal-habitat and matrix, allowing different species to have different habitat associations (Nabe-Nielsen et al., 2010; Betts et al., 2014; Chetcuti et al., 2019). The simulation included different species, in the baseline model defined only by unique identifiers. These species were simplistic, and did not have complex reproduction with seasonality, instead focusing on the interaction of the species with the landscape and if with their simple movements fragmentation could have both a negative and positive relationship on species diversity. In the two more complex models, I varied habitat-biased movement and habitat-modified mortality. To each species, I assigned a random rank from one (most suitable) to eleven (least suitable) to the eleven land covers. Preference, dependence, association or ranked suitability are simply the rank the species would choose the land cover, or comparatively how suitable they would find different land covers.

Individuals moved with a random walk in the baseline and a habitat-biased random walk in the other scenarios. An individual chose a point within a circle of random size up to a maximum distance around it, the emergent movement distance of this random distance is of a dispersal kernel (Figure 4-1) (Fahrig, 2001). The probability of individuals moving to any point in the circle was equal in the baseline model. In the other scenarios with habitat-biased movement, individuals were more likely to choose more preferred land cover. The simulation iterated through individuals in random order so that the simulation did not always assess the same individuals first within each time-step. 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. To simulate density-dependent mortality, if an individual counted more than two individuals were in the same cell, it died. This too was a simplification, the simulation can be run with more complex density dependence, varying within and between species density dependence, but in the pursuit of exploring the possibility of both positive and negative effect of FPS in species diversity, I opted to keep the simulation simple at this stage. Density dependence could be explored in future analysis. The habitat-biased movement and mortality both used a logistic function defined by a midpoint and slope to determine a multiplier between zero and one for each land cover (Figure 4-3). The multiplier for habitat-modified mortality increased the probability of dying in a time-step for individuals in less suitable land covers but death was not certain. The habitat-biased movement multiplier modified the probability of moving into a cell of a habitat, giving bias towards preferred habitat, but still allowing individuals to move into other land covers. Each individual did this by counting the cells of each land cover in the circle around it and multiplying these by the bias multiplier. Each land cover was then assigned a proportion of values between zero and one and a random number generated between zero and one selected a land cover (Figure 4-2). The individual then moved to a random point of that land cover within the circle.

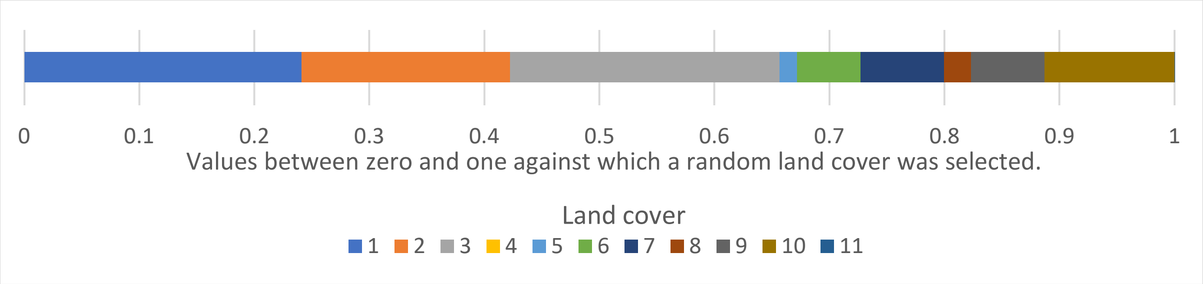


Figure 4-2. A representation of how each individual chose where to move to in a time-step. It did this by multiplying the proportion of each land cover in a circle around it up to the maximum movement distance, by the bias multiplier. The values were normalised and stacked and then a random number between zero and one was drawn which selected the habitat. The individual then moved to a random cell of that habitat within the maximum movement distance.

I chose a maximum movement rate of individuals of five cells per time-step and 5×10^{-4} chance of reproducing during a time-step. These arbitrary values would be realistic for different species. For example, based on allometric equations (Sibly et al., 2013) this could be, if a cell was a meter and the time-step a minute, ~5 m per minute and ~260 offspring a year (525,600 minutes in a year × $5\times10^{-4} = 260$) for invertebrates, or if a cell was a kilometre and the time-step an hour then ~5 km per hour and four offspring a year for birds or mammals. To stop my simulation from running longer than the 24-hour time-limit of the JASMIN HPC cluster LOTUS (Lawrence et al., 2013) I used, I chose a limiting carrying capacity of 4000 individuals in the landscape. I implemented the carrying capacity by increasing the chance of an individual dying when numbers were higher than the carrying capacity. Individuals could perceive the other side of the landscape over the edge of the landscape (i.e. “wrap-around” edges). I added an additional bounding area around the edge of the landscape of 10 cells wide with each cell in the area being randomly assigned a different land cover, to prevent species with bias from being influenced by the other side of the landscape. Individuals that left the landscape died.

4.3.3 Modelled scenarios

I generated 400 species per simulation run. In the baseline scenario, all had identical mortalities, fecundities and movement abilities, and with no habitat suitability. In the other two models, species’ ranked habitat suitabilities were generated separately for each simulation run using the R packages ‘gtools’ (Warnes et al., 2018) to permute the order of the vector 1:11 to give a rank for each land cover and ‘prodlim’ (Gerds, 2018) to exclude repeating a particular ranking within a simulation run. For the habitat-dependency model, each species had movement and mortality modified by their habitat suitability (Figure 4-3). In the specialism scenario, I compared the effect of FPS on specialists and generalists. In this case, I created 200 of each type of species

(400 in total), using the values in Figure 4-3 for the logistic slope for habitat bias and mortality. The species with a slope value of one, specialist species, had higher bias towards more suitable land cover but higher mortality in less suitable land cover than the species with a slope of 0.5, the generalists.

I carried out preliminary simulation runs without varying FPS, using a land cover that contained four patches. I used these runs to calibrate the model, choosing values for habitat movement bias and modified mortality that led to as high a number of individuals as possible while allowing the simulation to run for 200,000 model time-steps. This time allowed for the number of species to reduce to close to the equilibrium number of species (i.e. if the model ran until no more species were lost).

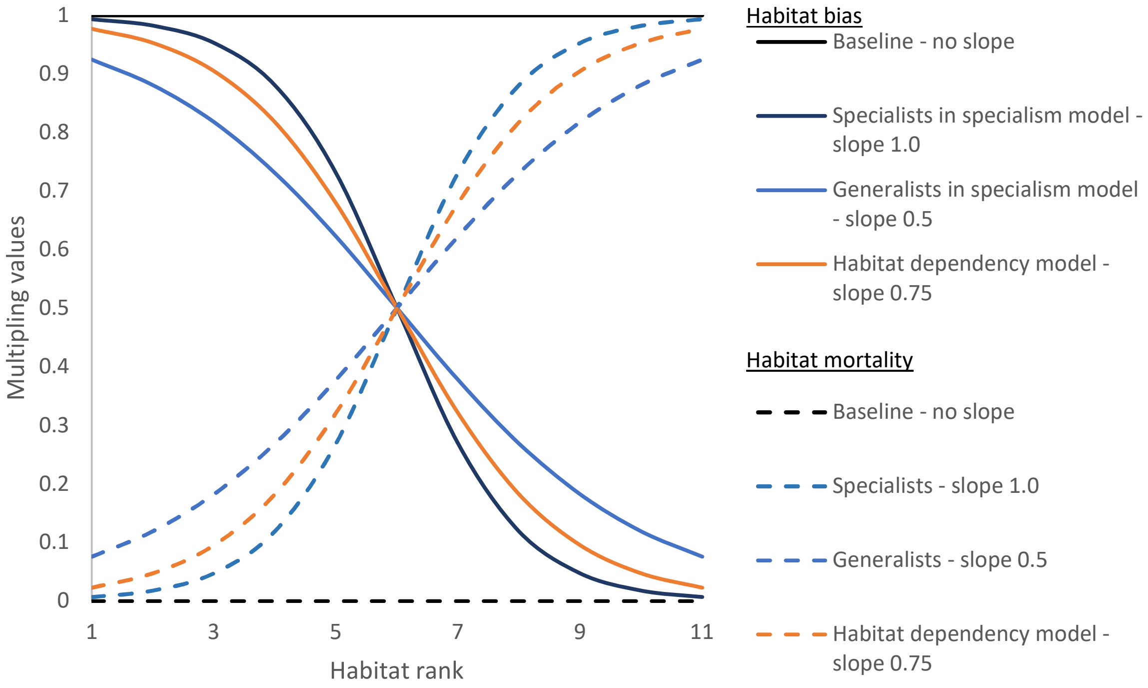


Figure 4-3 Values used for the logistic slope within each scenario for habitat-biased movement and mortality. The graph shows the effect the slopes have on the multiplying values used to bias the movement towards more suitable land cover and to increase mortality in less suitable land cover. There is mortality due density-dependence and from being over the carrying capacity of the whole simulation. The habitat-modified mortality is additional mortality above the normal levels. To link levels of additional mortality to that of the reproductive rate, the habitat mortality is multiplied by the reproduction rate 5 × 10-4 to give the additional amount of mortality. I used the same scenarios and values for 10% and 40% cover simulations. The specialist species were more competitive in more suitable land covers than the species in the habitat-dependency model and those more so than the generalists. Competitiveness was reversed in less suitable land cover.

4.3.4 Alpha-, beta- and gamma-diversity

I calculated diversity scores for the focal-habitat only, land cover one, reflecting the focus on FPS impacts. At the end of the simulation, I counted species within each patch of the focal-habitat. I then calculated the focal-habitat gamma-diversity, mean alpha-diversity per patch and mean pairwise (between pairs of patches) beta-sim-diversity (Barwell et al., 2015) using the R package ‘vegan’ (Oksanen et al., 2019). I used beta-sim-diversity as it is considered the best metric for presence-absence data and is unaffected by sample size which could be an issue as my patches got smaller with FPS and therefore included fewer individuals (Koleff et al., 2003; Barwell et al., 2015). For the habitat-dependency and specialism models, I classified species into three groups: high suitability, those for whom the focal-habitat was highly suitable (rank one to three); low suitability, (rank nine to eleven); and moderate suitability (all other species), which was a bigger group and could contain more species.

4.3.5 Analysis of results

I analysed the data using generalized linear models for gamma- (with a Poisson distribution) and alpha-diversity (with a gamma distribution), and beta regression for beta-diversity (‘betareg’) (values between zero and one) (Cribari-Neto and Zeileis, 2010) as affected by the number of patches (logged in the case of the beta-diversity, see Supplementary Information), as a measure of FPS. Differences between pairs of scenarios were tested by including both scenarios and creating interaction terms. Due to the simulation nature of my study, using p-values is not advisable (White et al., 2014). I instead focus on effect size and 95% confidence intervals. The effect size is usually over an increase of a unit of the independent variable. In my study this would be a patch but this is meaningless. It is more appropriate to consider the effect size over the range of FPS simulated. I calculated the effects over the range of FPS using the R package ‘effects’ (Fox, 2003; Fox and Weisberg, 2019).

4.4 Results

Considering all species found in the focal-habitat, gamma-diversity increased with FPS in all models. In the baseline model, habitat type did not influence movement or mortality, and I observed that individuals became scattered randomly across the landscape. But individual species became concentrated by chance in different locations through random movement combined with reproduction, and conversely, became vacant from other parts and this led to increasing beta-diversity with FPS (Supplementary Figure C4.1). Because the species were equivalent in the baseline model, individual species only went extinct through stochasticity. The gamma-diversity, therefore, remained high after the 200,000-time-steps of the simulation. In the baseline model the 95% confidence interval includes negative values and the effect size was low (Figure 4-4). The positive effect of FPS showed an increase for the habitat dependency and specialism models, of 2.7 and 4.5 species over the full range of fragmentation. In the latter models, the mean pairwise beta-diversity between patches increased faster than mean patch alpha-diversity declined. When the focal-habitat had low FPS, beta-diversity was low, as the few large patches contained similar sets of species. As FPS increased, beta-diversity increased because there were more patches, and these were in different landscape settings that suited different sets of species. In the baseline model, the movement and mortality of species did not differ among the land covers, and so the species existed as though there were no different land covers/habitats and distributed across the landscape through stochastic processes only. Therefore, more patches in different landscape settings made no difference to the beta-diversity in the baseline model and gamma-diversity only increased slightly due to sampling more of the landscape (+0.69). All results were the same for high (40%) and low (10%) overall focal-habitat cover (Supplementary Tables A C4.1, C4.2 and C4.3). I present results for 10% cover results here, while those for 40% cover are in Supplementary Tables A C4.4, C4.5 and C4.6.

The habitat-dependency and specialism models had differences in habitat-dependent mortality and movement bias among species. This led to lower gamma-diversity values as the species were more rapidly sorted in space and species less suited overall to the specific landscape of a simulation run died out. In these models, I observed that particular species became concentrated in areas of the landscape through habitat associations (Supplementary Figure A C4.1). In many cases, a few species dominated a single land cover patch. In the specialism model, the gamma-diversity of the specialists and generalists together summed to give a higher overall gamma-diversity than in the simpler habitat-dependency model in which species showed no specialism (Figure 4-4).

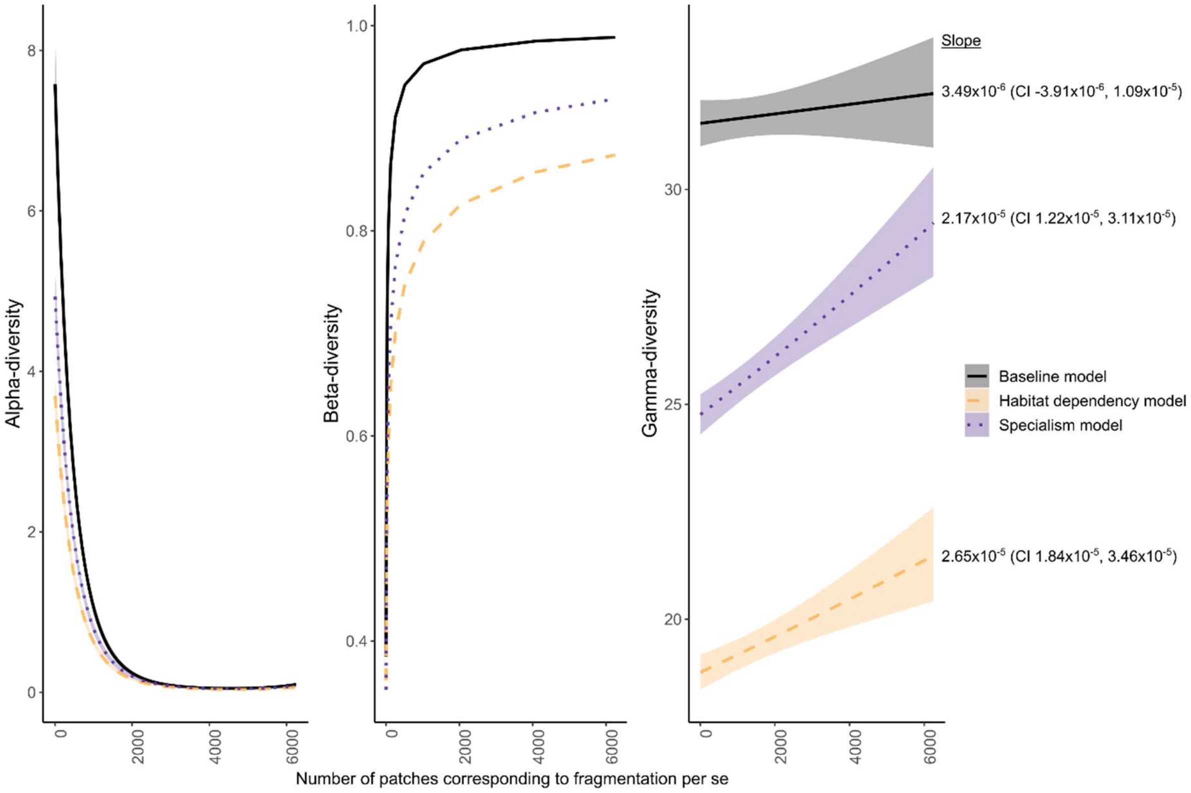


Figure 4-4 Mean patch scale alpha-diversity, mean pairwise beta-diversity and gamma-diversity for all species in the focal-habitat at 10% cover, with fitted lines and standard errors. Gamma-diversity increased with the number of patches (albeit not greatly for the baseline model), which represents FPS. In all cases, alpha-diversity declined, and beta-diversity increased.

Considering the different species groups in the habitat-dependency model, the gamma-diversity of the species for whom the focal-habitat had low or moderate suitability increased with FPS (Figure 4-5). This was as expected, as the increased edge-to-area ratio under FPS would mean more of these species drifted into focal-habitat patches by chance. The gamma-diversity of species for whom the focal-habitat had high suitability declined with FPS. The reduction in gamma-diversity over the whole range of FPS was again quite small, 2 species, although this is a 25% reduction. This reduction was also due to a greater amount of edge. In this case this greater edge meant these species were more likely to leave focal-habitat patches and also to be excluded from these patches by the influx of those species for whom the focal-habitat had low or moderate suitability.

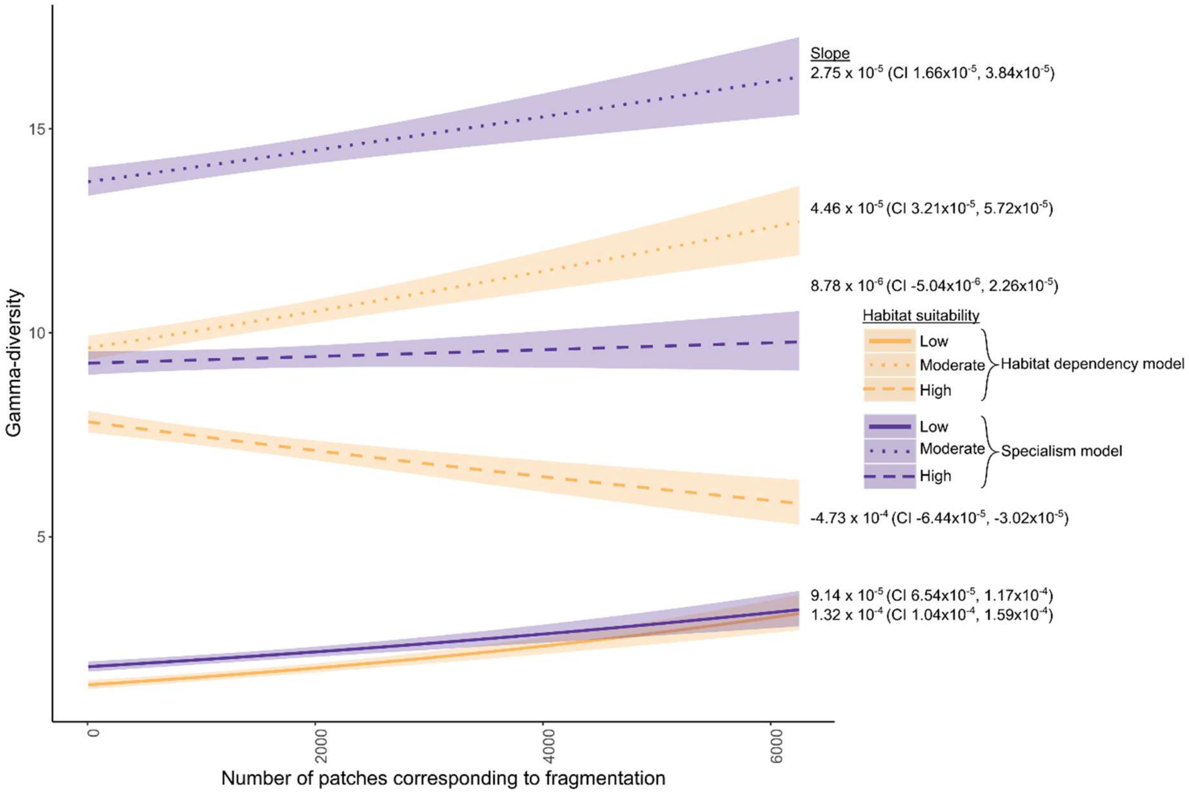


Figure 4-5 Gamma-diversity for three groups of species – those for whom the focal-habitat had high, moderate, or low suitability – for the habitat dependency model (habitat bias and mortality slope 0.75) and specialism model (habitat bias and mortality slope 1 and 0.5 respectively). Gamma-diversity increased with FPS in both models for the species who for whom the focal-habitat had low or moderate suitability, and those for whom the focal-habitat had high suitability in the specialism model. By contrast, in the habitat dependency model, gamma-diversity declined with increasing FPS for the species for whom the focal-habitat had high suitability.

In the specialism model, the gamma-diversity of the species for whom the focal-habitat had high suitability neither increased nor decreased with FPS. In contrast to the habitat-dependency model, the specialist species were more competitive in land cover to which they were suited, so they were better able to resist species that found the land cover less suitable and their beta-diversity increased at a rate greater than the decline in alpha-diversity, so gamma-diversity did not decline (Figure 4-6). The generalist species for whom the focal-habitat had high suitability also did better under high FPS than the species in the habitat-dependency model (which had neither specialists nor generalists), as they were able to use more of the wider landscape.

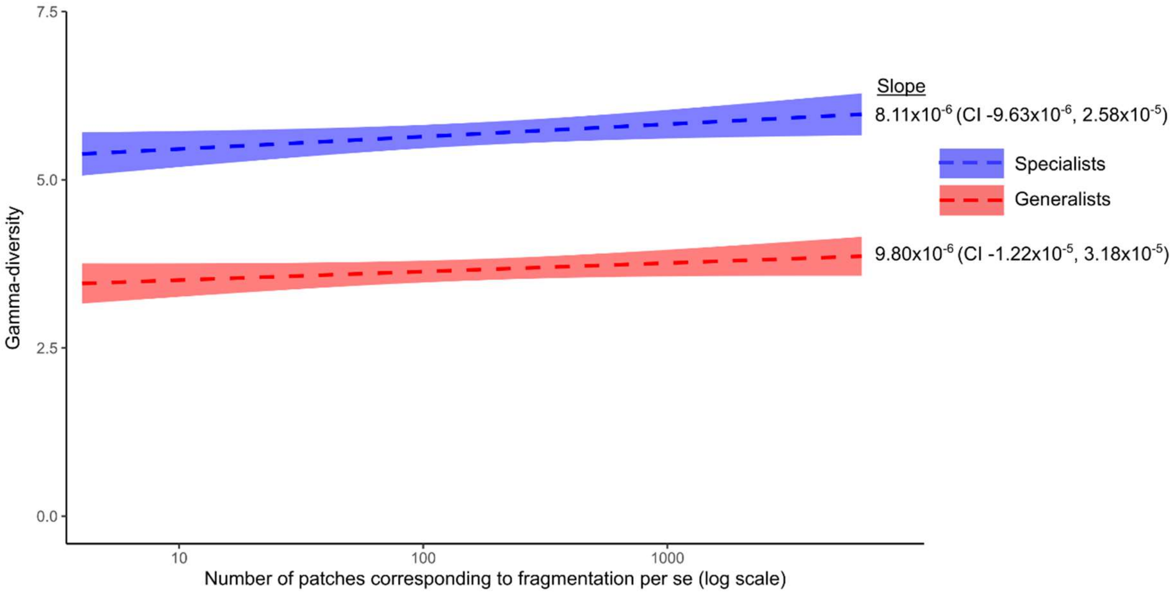


Figure 4-6 Gamma-diversity for those species for whom the focal-habitat had high suitability for the specialism model (habitat bias and mortality slope 1 and 0.5 respectively) showing specialists and generalists separately. Gamma-diversity increases with FPS for both specialists and generalists in all cases.

4.5 Discussion

This study helps to reconcile the debate on the effects of FPS on biodiversity (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019; Thompson et al., 2019). FPS had no effect or a positive effect on overall gamma-diversity of the focal-habitat across a landscape, but the gamma-diversity of species for which the land cover had high suitability could decline with FPS depending on specialism and competitive ability. Looking at the fragmentation threshold hypothesis was a small part of this study and unlike the SLOSS analysis of Rybicki et al. (2019) I found no difference in the relationship of gamma-diversity to FPS at 10% and 40% cover.

I found that beta- and gamma-diversity increased overall even without the species showing habitat specialisms. I did find that gamma-diversity of species for whom the focal-habitat was highly suitable declined with FPS, except in the specialism model where these species did not decline. In the habitat-dependency model, the species for whom the focal-habitat was highly suitable were under pressure by the influx into the fragmented patches by species for whom the land cover was less suitable, and the beta-diversity increase did not outweigh the loss in alpha-diversity, so gamma-diversity declined.

In the specialism model, the specialists were more competitive against other species in the focal-habitat and therefore beta-diversity increased at a similar rate to alpha-diversity decline, resulting in gamma-diversity not declining with FPS. The generalists did not decline, probably due to competitive release, or as they were better able to use multiple land covers outside of the focal-habitat. The implication of this finding is that FPS might have a negative effect on gamma-diversity only under specific circumstances. For example, if the quality of the focal-habitat declines, the species that are highly suited to the focal-habitat may act like those in the habitat-dependency model, with reduced competitiveness. With gamma-diversity being similar irrespective of the difference in competitiveness at low FPS, the difference in competitiveness may not have had an effect in the absence of FPS. But, as FPS increases its effects would interact with the lower land cover quality to cause these species to decline. Future studies could conduct simulations with complex assemblages of species or look at FPS together with other pressures on the species.

Because the habitat dependency and degree of specialism of species were so important in changing the direction of the relationship of gamma-diversity to FPS, information on species' habitat relationships are critical to planning landscape-scale conservation. In terms of conservation, it is often the less competitive species, with high dependencies on specific land covers that are of highest concern and that are the targets for conservation (Manchester and Bullock, 2000; Carrete et al., 2010; Fletcher et al., 2018). The effect fragmentation has on these species should, therefore, be assessed and the landscape managed to conserve these species. Doing so will have consequences for species in other habitats, however, and the resulting trade-offs should be analysed and considered. Fragmentation per se creates smaller patches, which have lower mean alpha-diversity as shown in my modelling. Lower alpha-diversity has a negative effect on ecosystem functioning at the patch scale, but beta-diversity has been suggested as important at a larger scale in supporting multiple ecosystem functions (Mori et al., 2018).

I generated species and land covers at random, meaning my results are widely applicable but not specific to any real landscape or communities. My simulations do not show whether particular species would be retained with increasing FPS. I used a large pool of potential diversity providing each simulation run with 400 randomly-generated species. I also randomly generated the land cover matrix between the patches of the focal-habitat, always having ten other land covers. Given the importance of the intervening land cover matrix in determining what species are in the landscape and how species move between patches (Brodie and Newmark, 2019; Chetcuti et al., 2019), future studies might look at the matrix specifically, non-randomly generating land cover matrices and including different mixes of anthropogenic and semi-natural land covers (Fletcher et al., 2018). My baseline model represented movement as a random walk, and I introduced bias based on habitat suitability in the more complex models. In reality, many organisms show complex movement behaviour (Gurarie et al., 2016), which is likely to be important in modelling how FPS affects biodiversity and could be a focus of future research.

My theoretical work studied FPS in heterogeneous landscapes, unpicking some of the mechanisms that can cause gamma-diversity to increase or decrease with FPS. Specialists and generalists did better than less competitive species that were highly suited to the focal-habitat. Less competitive species declined with FPS, as they were unable to hold out against increasing influxes of species for whom the focal-habitat had lower suitability. My research opens new avenues of research into how species demography and movement in relation to the focal-habitat affect biodiversity responses to FPS. Species' specialisms, habitat preferences and demography in different land covers (Chetcuti et al., 2019) should be taken into consideration when planning conservation as well as considering that under some circumstances FPS may lead to the conservation objectives of increased beta-diversity.

Chapter 5 **Matrix configuration mediates effect of habitat fragmentation: a modelling study**

5.1 Abstract

The conversion of land for human use has fragmented natural habitats. While habitat loss has clear negative effects on biodiversity, there is debate over whether fragmentation per se (FPS), which excludes the impacts of habitat loss, reduces species diversity. Fragmentation studies tend to use landscapes of fragmented focal-habitat and a single vastly different species-poor intervening land cover (the matrix). This is sensible when looking for an effect and when studying extremely degraded landscapes. But is this result generalisable to other landscapes, for example where the matrix is less hostile or degraded?

I used an individual-based model to investigate the effect of different configurations of the matrix land covers on the relationship between FPS and species diversity. I manipulated the number and quality of matrix land covers, and their similarity to the fragmented focal-habitat. I found that one aspect of the typical experimental design used in field studies, that of an extremely different matrix land cover, caused an order of magnitude stronger effect on alpha- and gamma-diversity and caused beta-diversity to decline with FPS. With low FPS, gamma-diversity was very high. Increasing FPS caused a dramatic decline to exceptionally low diversity. This was not the case in landscapes with a more moderate matrix; these had lower diversity under low fragmentation and declined little with increasing FPS. Furthermore, having a low number of matrix land covers caused beta-diversity to decline compared to having a larger number of land covers, except where the matrix was very similar to the focal-habitat.

My study has shown that the effects of FPS on biodiversity can change depending on the number of matrix land covers present and their similarity to the focal habitat. I recommend that fragmentation studies should consider a greater variety of landscapes other than only the vastly different focal and matrix land covers that are currently used. Doing so may help in showing cases where FPS does not have a negative impact and allow better predictions of the impacts of FPS. My study also highlights the importance of matrix land covers diversity and the benefits of improving the hospitability of matrix land covers for species dependent on the focal-habitat.

5.2 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; Fahrig, 2017; Fahrig et al., 2019). In reality, fragmentation and loss of habitat are intrinsically linked (Fletcher et al., 2018). Nonetheless, separating the effects of FPS from those of area loss by dividing habitat into more smaller patches and defining under what circumstances FPS leads to higher or lower species diversity are important for conservation decisions, such as restoration of habitat networks (Isaac et al., 2018).

One suggestion has been that results 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 reflected in landscape-scale biodiversity changes (gamma-diversity) (Fahrig, 2017; Fahrig et al., 2019). Patch-scale studies do not allow for 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, though 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. Patch-scale empirical studies, as well as many simulation 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 design therefore also inhibits the positive mechanisms of FPS, of 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 these landscapes. However, does the effect of fragmentation hold true for different, possibly less extreme landscapes such as between native woodland, plantations and scrub or between natural heaths and grasslands? What effect will using a matrix that is less species-diverse have on the effect of FPS? Using a species-poor matrix may lead to a reduced effect of competition on focal-habitat-species (Miller-Rushing et al., 2019) or allowing 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 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; van der Hoek et al., 2015; Fahrig, 2017). The matrix influences species persistence in the landscape by subsidizing resources, and with more similarity to the focal-habitat facilitating movement (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 (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 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 fragmentation per se in different landscapes (Fahrig et al., 2019).

Including more complex matrix configurations has been criticised for similar reasons to those suggesting a move away from considering simplistic landscapes. The worry is that non-habitat can provide resources and 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 land covers 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 a habitat associations (Chapter 2, Bollmann et al., 2005; Betts et al., 2014; Brodie and Newmark, 2019). 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 covers and have meta-populations in the new fragments of habitat. My approach continues to consider the fragmented habitat from the perspective of a human classified land cover, but also utilises a benefit of *individual-based modelling* (IBM) by allowing species-level perspectives, with different species having different associations with the focal-habitat and matrix land covers.

I have created a multi-species and landscapes simulation in the form of an IBM (see model description protocol, the ODD in chapter 3). Because FPS acts differently on different components of biodiversity, I use my 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 chapter, I configure the matrix differently by varying the number, the associated species diversity, and the similarity of the matrix land covers compared to the focal-habitat. I test the following hypotheses. 1) A matrix which is more dissimilar to the focal-habitat will lead to a stronger effect of FPS while a more similar matrix will lead to higher alpha- and gamma-diversity but lower beta-diversity and a lesser effect of FPS. 2) Matrix land covers which support more species will cause a strong decline in gamma-diversity of the focal-habitat-species in the focal-habitat with FPS because of greater influxes of tourist species, and therefore higher competition, into the patches as they become fragmented. 3) An increase in the number of matrix land covers increases gamma-diversity due to higher beta-diversity. Under low FPS this will lead to there being more land covers 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 matrix land covers, leading to increasing beta-diversity with FPS and so a lesser decline in gamma-diversity.

5.3 Method

My multi-species and landscapes simulation (Figure 5-1) 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 has been described following the ***O****verview,* ***D****esign concepts,* ***D****etails* (ODD), protocol for describing individual- and agent-based models (Grimm et al., 2006; Grimm et al., 2010). To aid the readability of these Methods, the ODD is placed in chapter 3. Each model and landscape configuration was repeated 50 times. This resulted in 7000 simulation runs.

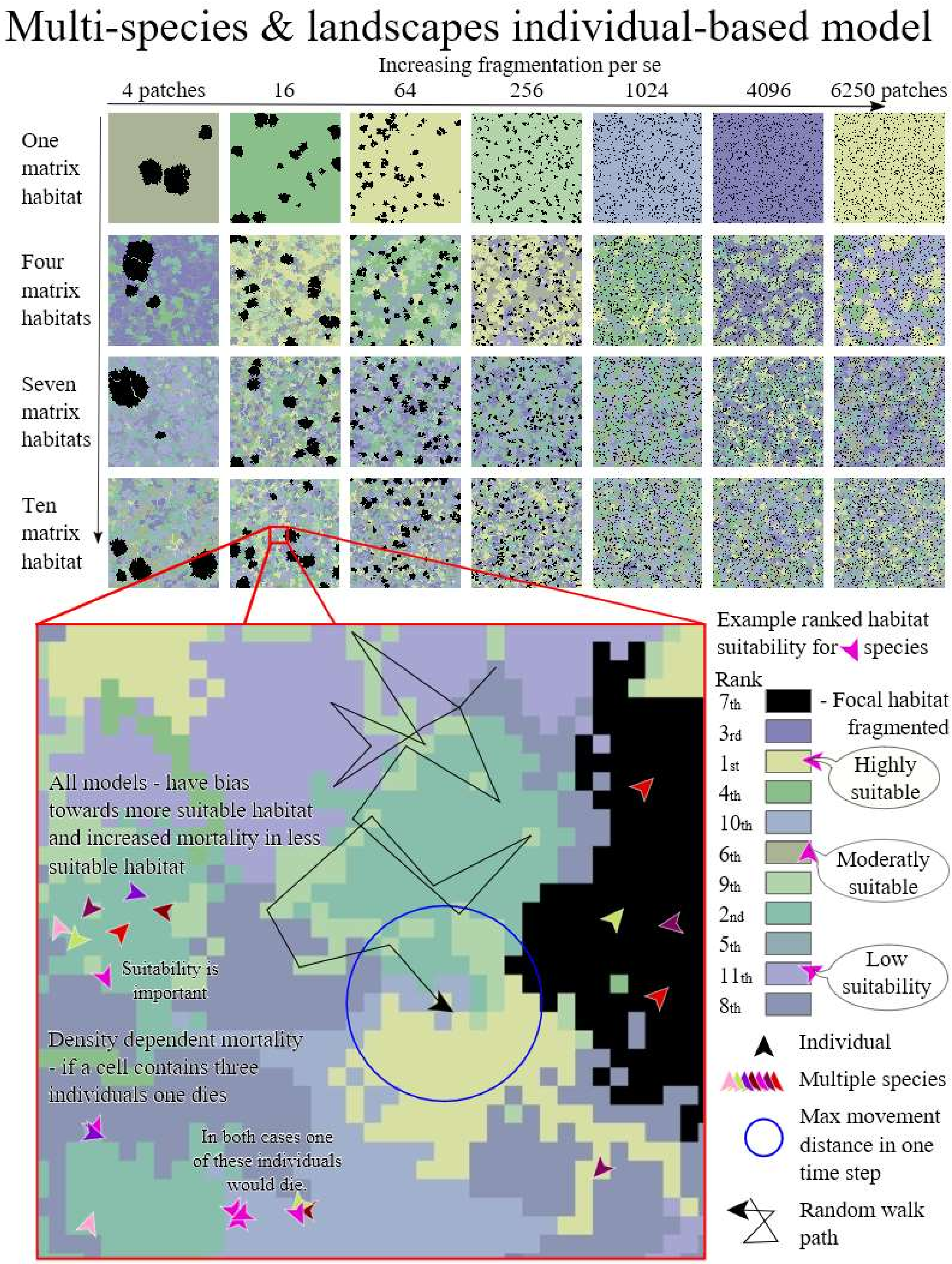


Figure 5-1 A figurative description of the individual-based model, showing how I represented FPS by increasing the number of patches of the focal-habitat (in black) while keeping its total area the same and that I looked at a differing number of matrix land covers. I give an example of the ranked suitability for 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 land covers according to their assigned suitability, with habitat-modified mortality and individuals showing biased movement.

5.3.1 Land cover FPS and matrix land cover diversity

In this study, I simulated land covers in which I 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, using the same method as in chapter 4 (Figure 5-1). I created increasing FPS by simulating land cover data with 4, 16, 64, 256, 1024, 4096 and 6250 focal habitat patches while keeping the area at 10% (based on the results from chapter 4) of the 1000 × 1000 cells of land cover. I also varied the number of land covers in the space in-between the focal-habitat patches, the matrix. I did this by creating 1, 4, 7 or 10 matrix land covers. Combining variation in FPS (7 treatments) and the number of matrix land covers (4 treatments) gave 28 different landscape types. For every landscape simulated, I also created a dataset that defined patches in that landscape. I defined each patch as a contiguous area, including those connected by corner cells, of a land cover. The landscape for every single of the 7000 simulation runs was different as I generated each landscape and corresponding patch dataset individually for each replicate and model scenario. I did this to capture variations in the landscapes.

5.3.2 Simulation

I used the same multi-species landscape simulation as in chapter 4. I defined the species differently for different scenarios, but I 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 a particular taxon. The only characteristic of these species was that they move and are differently suited to the different possible land covers in the landscape. Species are still simplistic focusing on their relationship to the landscape to focus in on how their relationship to the matrix land covers will influence the effect of habitat fragmentation. I defined the distinct species by how suitable they found different land covers in the landscape. I defined each species in terms of suitability for the eleven land covers irrespective of the number of matrix land covers in a particular run of the simulation (1, 4, 7, or 10). I defined this habitat suitability by ranking each of the eleven land covers with values between one and either eleven or twenty-three depending on the experimental scenario. One of the scenarios used a ranking of the eleven land covers from one to twenty-three to increase difference between land covers, I explain this in the description of that model. I generated species randomly as there are too many combinations of species to represent all ways of defining species. By randomly creating species, I captured the variation across different sorts of species. I generated the species separately for each repetition and landscape. I define focal-habitat-species as those species for whom the focal-habitat is most suitable (habitat suitability rank one).The huge combination of possible species within this simulation, is further justification for keeping the species simple as adding in further complexity at this stage would lead to difficulty in interpreting results.

All organisms moved with a habitat biased random-walk, meaning they could choose to move to cells within a five cells radius, including corner cells, around themselves but had a higher probability of choosing land cover which they find more suitable. The individuals had habitat-biased movement and habitat-modified mortality equivalent to the habitat dependency scenario in chapter 4, although one of the scenarios in the current study defined this over a different number of land covers to achieve differences in the similarity between the focal and matrix land covers. I defined both the habitat-biased movement and modified mortality as logistic curves that related habitat preference and suitability to a value between zero and one that increased the probability of choosing a preferred land cover and increasing mortality in less suitable land covers within the simulation. I use suitability to represent both preference 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 (Figure 5-2).

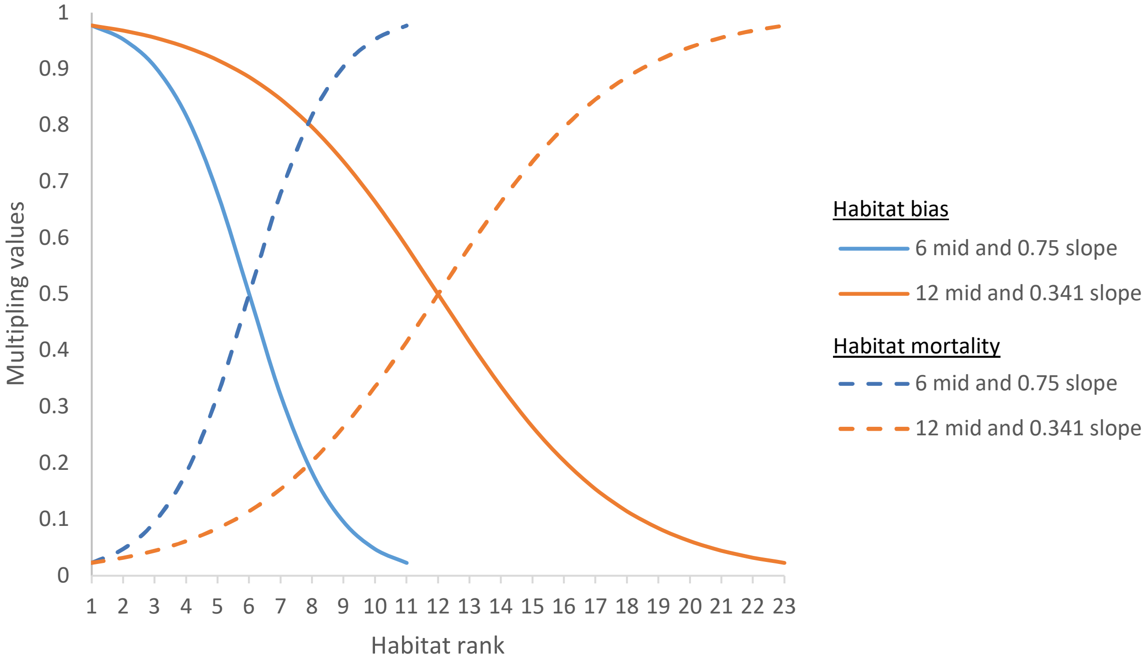


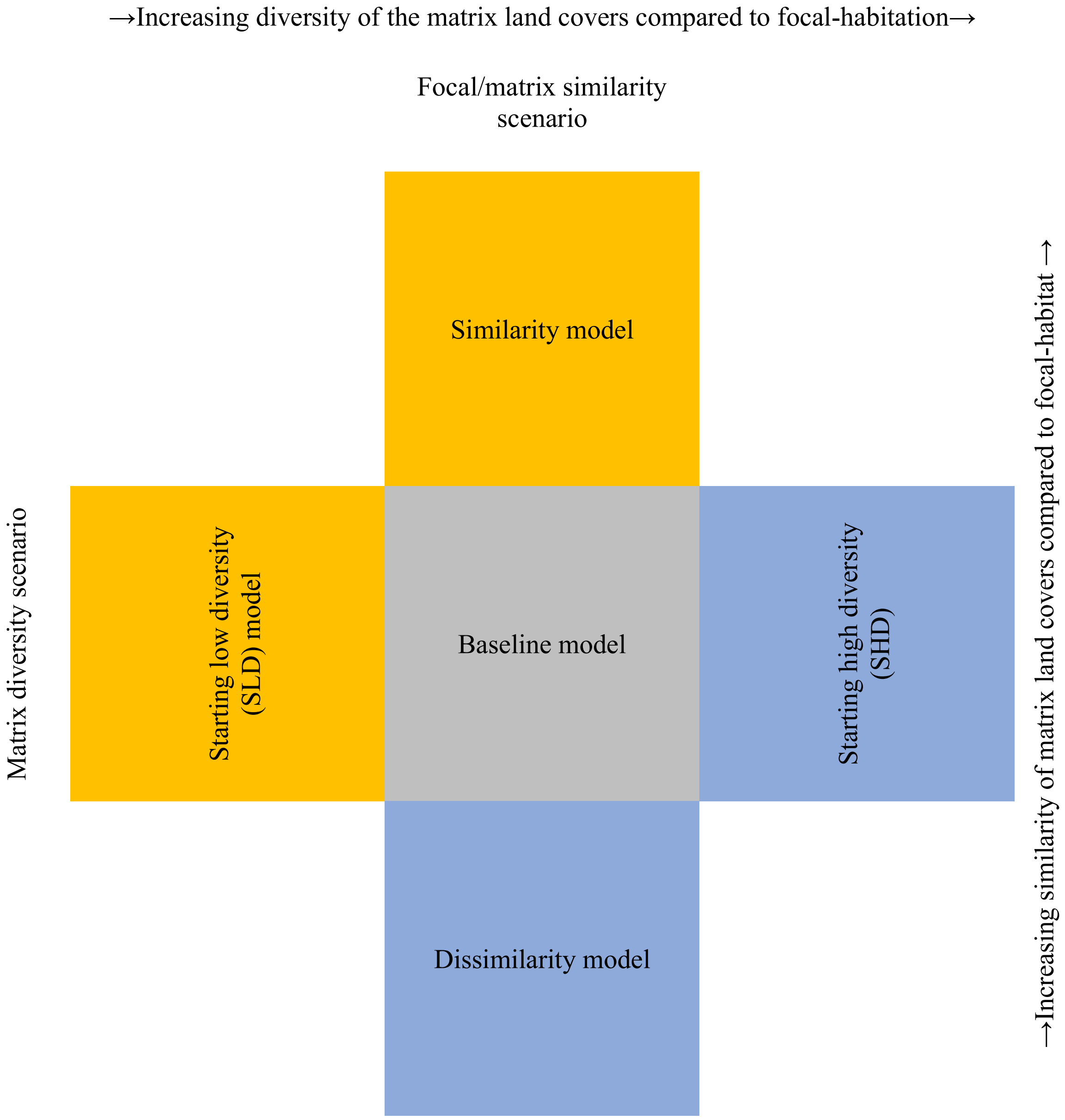
Figure 5-2 Values used for the logistic slope within each experimental scenario for habitat biased movement and mortality. The baseline model and the two models in the matrix diversity scenario used the curves in blue with a midpoint of six and a slope of 0.75. The two models in the focal/matrix similarity scenario used the orange curves with a midpoint of 12 and a slope of 0.341, to make the matrix 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 and to increase mortality in less suitable land cover. There are universal mortalities from density-dependence and from being over the carrying capacity of the whole simulation. The habitat mortality is additional mortality above the normal levels. To link levels of added mortality to that of the reproductive rate, I multiple the habitat mortality multipliers by the reproduction rate 5×10^{-4} *to give the added probability of mortality.*

The boundary of the simulation was different to that in chapter 4, in which individuals leaving the simulation died. Instead, the boundary was toroidal with individuals able to cross over the edge and reappear on the other side of the landscape. I made this change because I observed that with edge death the density was lower at the edges of the landscapes and higher in the middle. I also ran some additional analysis and showed that the habitat dependency model in chapter 4 had the same result (declining gamma-diversity with FPS), regardless of having mortality or not. I therefore chose to switch to a toroidal simulation. At the edge of the simulated landscape, I added a ten cell-wide strip to each side of the landscape, with each cell randomly assigned a land cover to avoid the land cover on the other side of the landscape influencing species into crossing over the edge or not.

5.3.3 Experimental scenarios

I applied two scenarios to the 28 types of landscape that varied according to focal-habitat FPS and number of matrix land covers. I compared the models in both scenarios to the same baseline model. I took the baseline model from the habitat dependency scenario in chapter 4 and specified that each matrix land cover would start equally diverse to the focal-habitat and that each land cover in the matrix could be similar or dissimilar to the focal-habitat entirely randomly. The first scenario, the focal/matrix similarity scenario, contrasted: 1) all of the matrix land covers being similar to the focal-habitat; and 2) all of the matrix land covers 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 as with the focal-habitat; and 2) double the number of species associated with each matrix land cover (Table 5-1).

Table 5-1 How the five models of the two scenario both relate 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.



5.3.3.1 Baseline model

In the baseline model, the midpoint of the logistic function used for the bias and additional habitat dependent mortality was 6 and the slope was 0.75 (Figure 5-2). I included this model to give initial insights into the effect of the number of matrix land covers on the relationships of diversity to FPS and against which to compare the models of the two scenarios. Forty species were most strongly associated with each of the eleven land covers, with the land cover species were associated with having a habitat suitability of rank one and the ranking for other land covers randomly assigned inclusively between two and eleven. This gave 440 species at the beginning of the simulation. Because for each species I assigned a random ranking for the eleven land covers the focal-habitat and matrix land covers were not universally similar nor dissimilar.

5.3.3.2 Focal/matrix-similarity scenario

The focal/matrix-similarity scenario included two models, the Similarity and Dissimilarity models. Specifying the two models of this scenario was more complex than the other scenarios. For land covers to be similar, species had to have similar multiplying values derived from the logistic equation for habitat bias and mortality, and for dissimilar land covers to have very different values (Figure 5-3). To do this I allowed the suitability for the eleven 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 I used to specify habitat bias and mortality for habitats based on the habitat suitability, remained approximately the same (0.98 and 0.02 respectively) (Figure 5-2). For the Similarity model, I assigned a rank to each species for each habitat suitability between 1 and 11 so that species would find the land covers to be similar to each other (Figure 5-3).

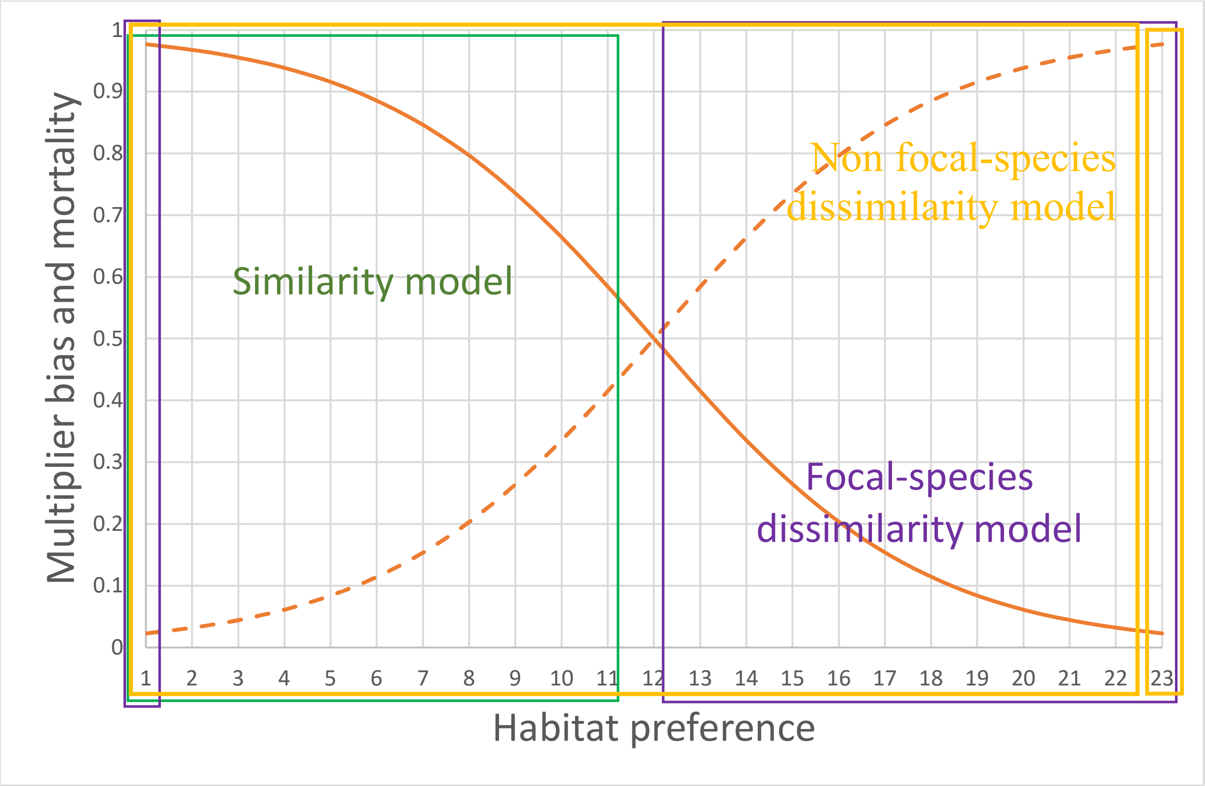


Figure 5-3 For the similarity model, the ranking for the eleven land covers was chosen from between one and eleven inclusively, shown in green, this meant the bias in solid orange and mortality in dashed orange were less different between the land covers. The dissimilarity model had focal-habitat-species 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 away 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.

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 (Figure 5-3). 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 low and the mortality in them was 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 covers. For the other nine matrix land covers, I assigned ranks between 2 and 22. All non-focal species had a rank of 23 for the focal-habitat. The nine other matrix land covers 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 only two 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 2 gives an example of suitability for the land covers for similar matrix and focal-habitat and dissimilar matrix and focal-habitat.

Table 5-2 An example of the habitats suitable rank for species, that made the focal and matrix land covers similar or dissimilar. Species 1 is a focal-habitat-species in both example models.

Similarity model

Land cover	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
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

Land cover	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
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
…	…	…	…	…	…	…	…	…	…	…	…

5.3.3.3 Matrix-diversity scenario

As in the baseline, the midpoint of the logistic function used for the bias and additional habitat-dependent mortality was six and the logistic slope was 0.75 (Figure 5-2). The matrix-diversity scenario included two models: 1) The Starting Low Diversity (SLD) model, where each matrix land cover had a lower species diversity at the beginning of the simulation than the focal-habitat and than in the baseline model, and 2) The Starting High Diversity (SHD) model, where each matrix land cover 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 was associated with half as many species, twenty compared to the forty in the focal-habitat; giving 240 species at the beginning of the simulation (10 × 20 + 40 in the focal-habitat). In the SHD model, eighty species were associated with each of the matrix land covers, giving a starting number of species of 840. I loaded these freshly generated 240, 440 or 840 species into each run of the IBM simulation at the beginning regardless of how many matrix land covers the simulation had.

5.3.4 Alpha-, Beta- and Gamma-diversity

At the end of each simulation run, I recorded the individuals in each focal-habitat patch. I 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). I did not look at species richness per cell because of the density dependence which would have meant that a cell could only have contained two species maximum. I calculated alpha-, beta- and gamma-diversity for focal-habitat-species only. I define the focal-habitat-species as the species for whom the focal-habitat is most suitable and who are dependent on focal-habitat. This chapter will focus on the effect on the focal-habitat-species. I focused on the focal-habitat-species because they are the species most strongly affected by increasing the FPS of their habitat (as part of the high suitability group in Chapter 4).

5.3.5 Analysis of results

I employed a similar analysis to that of chapter 4. I graphed results and performed regression analysis of alpha-, beta- and gamma-diversity with an increasing number of focal-habitat patches representing FPS and report effect sizes . I 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). I used beta regression for beta-diversity ('betareg') (Cribari-Neto and Zeileis, 2010) (values bound between zero and one). The beta sim values range between zero and one inclusively while beta-regression does not include zero or one themselves. To perform beta regression, I therefore scaled the values to be greater than zero and less than one (0.001 to 0.991). Where gamma-diversity values were zero I excluded the zero beta-diversity value as meaningless, the fitted relationships was nowhere near the datapoints and because they suggested a much larger difference between the SHD, SLD and baseline models; ultimately the results were very similar, but reduced in magnitude. I also excluded NA beta-diversity values. These NAs were due to an error that occurred when only one patch had species, with up to three species. These NAs should have been zero. Removing zeros and NAs removed 1861 records for the focal-habitat-species. To calculate alpha-diversity with a gamma distribution, I added 0.001 to the values to remove zeros. I tested differences between pairs of models by including both scenarios and creating interaction terms. Due to the simulation nature of my study using p-values was not advisable (White et al., 2014). I 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, this would be a patch in my study. In my study, this is not very meaningful, and it may be more appropriate to think of the effect size over the range of fragmentation simulated. I obtained predicted values for each of the number of patches used in my study to look at effect sizes by using the R packages ‘effects’ (Fox, 2003; Fox and Weisberg, 2019)

5.4 Results

For the focal-habitat-species, increasing FPS through increasing the number of patches of focal-habitat always led to a decrease in alpha- and gamma-diversity. Beta-diversity variously increased or decreased in the different models. 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 covers, did not change overall trends in alpha- or gamma-diversity of the focal-habitat focal-habitat-species. There were, however, differences in levels 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, unaffected or negatively affected by FPS. I will first present the results of the focal/matrix-similarity scenario which have the most extreme results, then the matrix-diversity scenario, and finally talk about the difference the number of matrix land covers made.

5.4.1 Focal/matrix-similarity scenario

In the models of the focal/matrix-similarity scenario (Figure 5-4), 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, the beta-diversity was unaffected by FPS (between -0.01 and 0.02), except when there were ten matrix land covers, when 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, and declined strongly in the dissimilarity model. The baseline model again, as it had for beta-diversity, showed a weak decline in gamma-diversity with FPS where there were few matrix land covers, and decreased more strongly with more matrix land covers. In Figure 5-4 and the corresponding beta regression, I did not include zero or NA values where gamma-diversity was zero as these are meaningless because with no species the patches are neither similar nor dissimilar, but beta-diversity still declined with FPS. These removed values would have had the largest effect on the dissimilarity model (903 records), and less on the baseline (295 records) and similarity model (166 records).

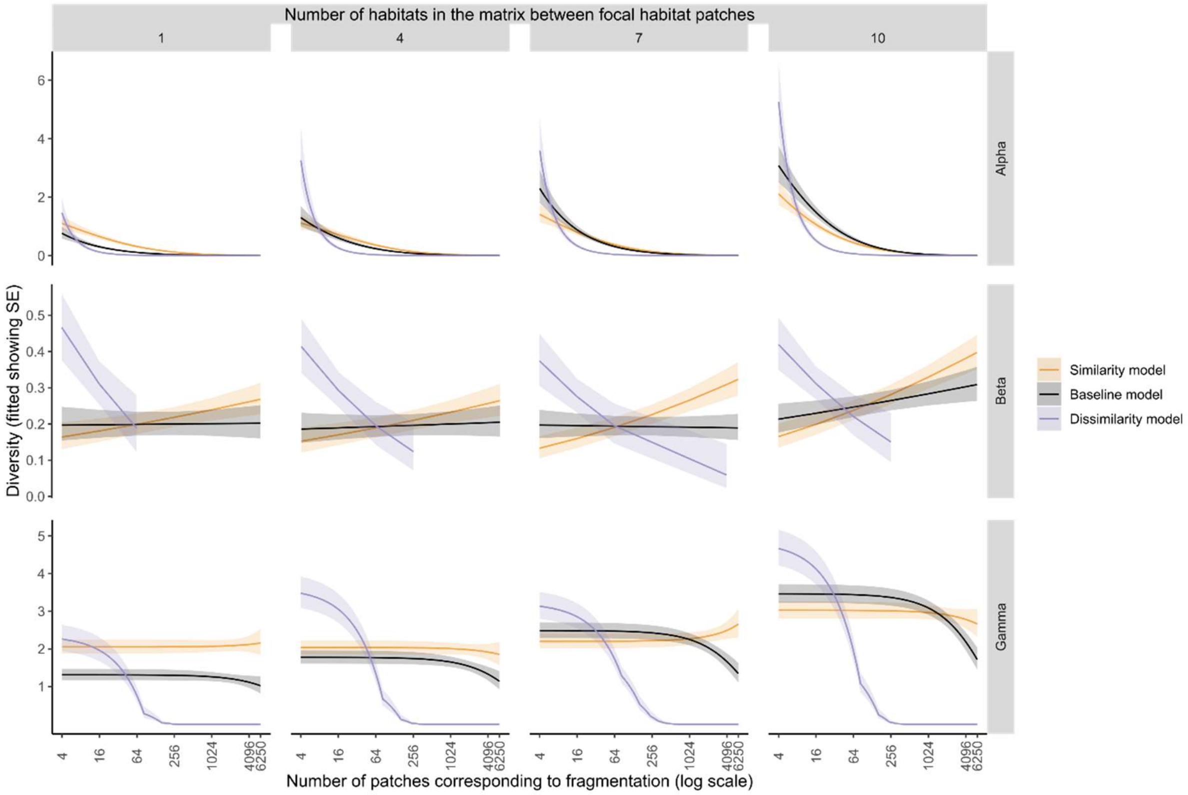


Figure 5-4 Change in alpha-, beta-, and gamma-diversity of the focal-habitat with FPS, for the focal-habitat-species for whom the focal-habitat was most suitable. The graph shows the results for the similarity, baseline (neither similar nor dissimilar) and dissimilarity models.

5.4.2 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), did lead to a difference in the species composition at the end of the 200,000-time-steps of the simulation. Like 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). 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, when it increased. This was similar for the SLD model, although possibly declining marginally with few matrix land covers (-0.02) and becoming marginally positive with ten matrix land covers (0.02). This again resulted in an overall decline in gamma-diversity with FPS, but only at high FPS. Gamma-diversity was higher with more initial starting species, again with the SHD model having the most, then the baseline model and the lowest with the SLD model.

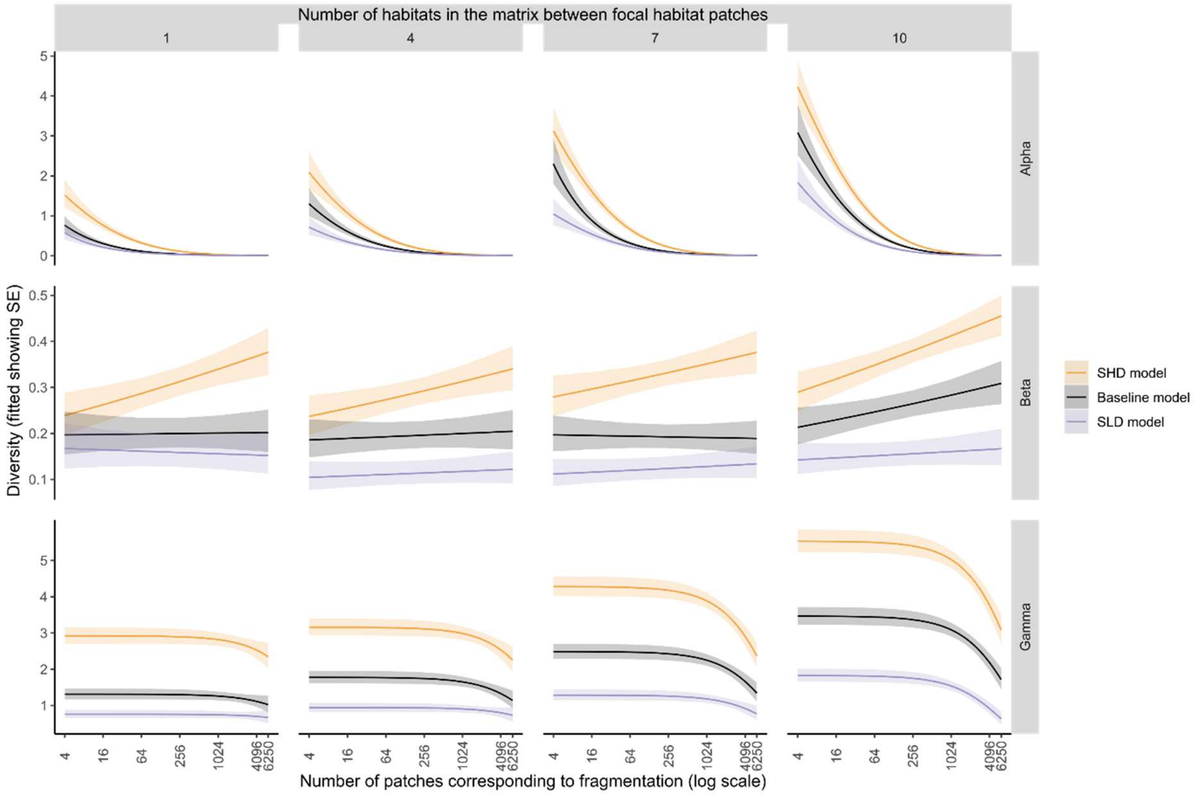


Figure 5-5 Change in alpha-, beta-, and gamma-diversity of the focal-habitat with FPS, for the focal-habitat-species for whom the focal-habitat was most suitable. The graph shows the results for the Starting Low Diversity (SLD), baseline (starting equally diverse) and Starting High Diversity (SHD) models.

5.4.3 Number of matrix land covers

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

5.5 Discussion

My study showed that FPS had a consistent negative effect on alpha- and gamma-diversity for species associated with the focal habitat. But the magnitude of the effect was much increased when the focal-habitat and matrix land cover were very different from each other. Fragmentation has been shown in another modelling study to have a lesser effect when matrix land covers are more similar (Hatfield et al., 2020). This dissimilar matrix and focal habitat design is often used for experimental landscapes in field and simulation fragmentation studies (Ewers et al., 2011; Haddad et al., 2017; May et al., 2019). Given my results, such designs could mask cases where other 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 in all types of landscapes and with all sorts of species (Galán-Acedo et al., 2019).

Alongside variation in which species (e.g. all *vs* habitat dependent) are counted (chapter 4, Miller-Rushing et al. 2019), 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, increases in beta-diversity caused by the positive mechanism of FPS, increased land cover diversity, cannot be accounted for. The species poor, very dissimilar matrix also further increases mortality, and drives down alpha-diversity. In chapter 4 I showed that gamma-diversity is unaffected by fragmentation in certain circumstances; in that case in a group that included the focal-habitat-species, when the simulation included specialist and generalists. Chapter 4 used ten matrix land covers and a setup similar to the baseline model used here, with the matrix land covers being neither similar nor dissimilar. The positive effect of FPS on beta-diversity and no effect on gamma-diversity of specialists and generalist species, may have been masked in studies using a dissimilar matrix and focal-habitat.

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 more land cover diverse can 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.

I found little difference in the effect of FPS by changing the species diversity of the matrix compared to the focal-habitat. 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 potential diversity of the matrix land covers and not the focal-habitat, did cause the alpha- and gamma-diversity of the focal-habitats to be higher. I had expected the opposite effect as I had hypothesised that more species in the matrix would also mean more of them would be "tourists" in the focal-habitat patches. I 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 carrying capacity, there was a greater diversity of non-focal species of the possible approximately 36 million non-focal species. These non-focal species had therefore a greater diversity of different rankings for different land covers. This could mean that there were more small areas occupied by species well suited to a mix of land covers in that area. Different focal-habitat-species may do better with different neighbours, therefore, as although species in this simulation do not exploit each other, they are more competitive or less competitive compared to each other. 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. The carrying capacity was applied over the whole landscape. Because of the movement bias, with more matrix species more species would show biased movement towards the matrix and species density could be higher in the matrix.

A caveat to the result that focal-habitat-species diversity was higher with initially higher matrix diversity is that all models ran for the same amount of time. Given more time the more diverse matrix may have fallen to similar levels of diversity to the baseline and then the SLD levels, at which point the diversity of the focal-habitat-species may have reduced. If this was not the case and the SHD model with a high starting diversity stayed higher, then, maintaining or enhancing the quality of the matrix to encourage diversity of species dependent on these matrix land covers may also help the diversity of the focal-habitat-species and mitigate fragmentation (Neilan et al., 2018).

I showed that a greater diversity of land covers, i.e. more matrix land covers, can lead 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 objective 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 covers have on focal-habitat species is important in fragmentation and connectivity research and planning (Fletcher et al., 2019). More matrix land covers reduced the effect of FPS in the dissimilarity model, but not to the degree of the baseline, similarity, SHD or SLD models. It is important to use matrix land covers that are not always highly dissimilar in future field and simulation studies of fragmentation. Having few matrix land covers was detrimental to beta-diversity, preventing it from increasing with FPS. Using more matrix land covers may be important when conducting field studies, particularly when looking for positive effects of FPS. I therefore agree with the call to move away from a binary landscape, as suggested by others (Valente and Betts, 2019). As I mentioned in chapter 4, beta-diversity has 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 habitat within a landscape.

Given the influence of the matrix land covers on the effect size of FPS on gamma-diversity, it may be a good idea 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). This 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 I 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). My species experience differences in mortality and 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 my species do not differ in their ability to move through different land covers. 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 from a woodland edge and refuse to travel 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 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. I do begin to explore differences in the way species move in the next chapter. I do this by changing bias and movement based on land cover, but even there I have not changed the rate of movement within land cover nor repeated the analysis of this chapter with these different walks.

My study has important implications for how to conduct future research into fragmentation. In this study, different configurations of matrix land covers did not change results on 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 habitat and matrix model than in all the other models. This suggests that this popularly used research landscape could overpower more subtle results. 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 show this difference, even at a patch scale, by using landscapes that are more varied with a diversity of matrix land cover types and not just an extremely different matrix land cover. Further, this study supports the need to safeguard matrix diversity of land cover and species within the landscape to lessen any negative effects of habitat fragmentation by safeguarding and improving matrix quality.

Chapter 6

Mobile species are positively affected by fragmentation per se

6.1 Abstract

Human conversion of habitat has led to habitat loss and fragmentation. The effects of habitat loss are confirmed, but the effects of habitat fragmentation per se (FPS), fragmentation without habitat-loss, are currently in debate. Both empirical and modelling studies of FPS show negative, neutral, or positive effects. These studies cover different sorts of species, with potentially different responses to FPS. There is a knowledge gap concerning how species characteristics determine their responses to FPS. For example, does FPS have more negative effects on species that spend more time in the matrix between habitat patches? Does functional connectivity increase with FPS for species with higher dispersal ability and therefore higher encounter rates of patches?

I created a multi-species landscape-scale individual-based model with simulated species who experience higher mortality in less suitable land cover. The species differ in walk type and can move with a random walk (RW), correlated random walk (CRW), or habitat dependent walk (HDW) and biased versions of these walks with increased habitat bias. RW individuals can move in any direction. CRW individuals can turn within a set of angles from the previous direction. HDW individuals consider the suitability of the current land cover and RW in preferred land cover and progressively more CRW in less suitable land cover. These walks modify how readily species can move between habitat patches. Increasing bias towards suitable land cover causes individuals to spend more time in suitable land cover and less time in the land cover falling between habitat.

Without bias towards more suitable land cover, FPS did not affect gamma-diversity. With bias, RW species declined with FPS but bias had little effect on species moving with a CRW. With moderate bias, gamma-diversity of HDW species increased with FPS. Yet, with high bias, they strongly declined. These results show that even for species that are dependent on the habitat that is fragmented, FPS does not have a universally negative affect. FPS can have a positive effect on species able to move between patches of habitat as their functional connectivity

increases. These results offer an explanation as to why fragmentation in the absence of habitat loss appears to show contradictory results in different studies.

6.2 Introduction

Many habitats have experienced large scale fragmentation and loss caused by conversion to different land covers and uses (Lawton et al., 2010; IPBES, 2018). While habitat loss has clear negative effects (Fahrig, 2003; Loke et al., 2019), there is debate over whether fragmentation per se (FPS), fragmentation without or while controlling for habitat loss, always has a negative effect (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019). Fragmentation is not always defined in the same way with many studies defining fragmentation as the converse of connectivity (Leroux et al., 2017; Bueno et al., 2018; Horváth et al., 2019; Brodie and Newmark, 2019). FPS comprises the splitting up of patches without a clear relationship to connectivity. Connectivity is defined as the facilitation of movement between patches of habitat, and measurable as the probability of individuals of a species moving between all patches of habitat (Taylor et al., 1993). Connectivity is, therefore, dependent on each of the species in the study. Connectivity is sometimes called functional connectivity to differentiate species connectivity from structural connectivity, which is the physical connectedness of contiguous areas of habitat that would be similar to a lack of fragmentation (Bélisle, 2005). It has been suggested that FPS could actually increase functional connectivity because the smaller patches will be closer together and more regularly scattered through the landscape than when less fragmented (Fahrig, 2017; Galán-Acedo et al., 2019). Thompson et al. (2019) looked at connectivity using their measure of effective connectivity measuring individuals' ability to disperse through fragmented landscapes and found that for the generic species simulated within their study fragmented landscapes were more connected than less fragmented landscapes.

Simulation studies have generally created species that move with a random walk (RW) (Fahrig, 2001; Rayfield et al., 2011) or correlated random walk (CRW) (Johnson et al., 1992; Boone and Hunter, 1996; Jepsen and Topping, 2004; McIntire et al., 2013). These movement types are often criticised as being too simple and unrealistic, and it may be more realistic to represent species as moving differently depending on the land cover they find themselves in (Kuefler et al., 2010; Wang, 2019) and therefore with a habitat dependent walk (HDW). Each modelled walk type is likely not a bad model for movement, but may represent the movement behaviour of different types of species (Da Silveira et al., 2016; Thomaes et al., 2018; Bérces and Růžičková, 2019; Fletcher et al., 2019). It may be that different field studies have had different proportions of species moving with different types of walk. I explore whether such differences could lead to differences in the effect of FPS. By defining species that move more or less directionally, with CRW, HDW, or RW (more to less directionally respectively), and by changing the bias towards more suitable land cover, species move between patches of focal-habitat more or less and spend more or less time in the matrix.

Moving between patches of focal-habitat by crossing the matrix is costly in terms of time lost from other activities and the risks of increased mortality (Bonte et al., 2012). Species spending more time in less suitable land cover will spend less time reproducing and incur higher mortality from less food availability, damage, and predation. Species who leave their habitat less often should be more successful, and in the short term, FPS should affect them less if they can survive in small patches. They may experience longer-term effects of isolation such as inbreeding depression if individuals of the species are unable to move between patches of habitat (Cosgrove et al., 2018). Species able to move between patches more readily may benefit from increasing functional connectivity between patches brought about by increased FPS. The functional connectivity will not be higher than if all the species were in a single large patch of habitat, but with increasing FPS over a small amount of FPS, functional connectivity will increase and allow for the separation of the population into more metapopulations. With higher FPS, having more small patches closer together may lead to a higher encounter rate and therefore less time in the matrix (Fahrig, 2017) while allowing for the spread of risk and for competitive release. Species are potentially at risk from extinction in the landscape as a result of the destruction of a single population in one location, and are safer having multiple sub-populations spread among different patches of habitat (Fahrig et al., 2019; Rybicki et al., 2019). Species may also benefit from competitive release with different competitor species occupying different patches at different times (Resasco et al., 2017).

I test two hypotheses from mechanisms proposed by Fahrig (2017): firstly, that FPS should affect species that spend more time in the matrix between patches of the fragmented focal-habitat more negatively than species that spend less time in the matrix; secondly, that FPS should affect species less if they have higher patch encounter rates and are able to traverse the landscape more easily. The latter of these if true would support the idea of increased functional connectivity for such species.

I use a multi-species and landscape-scale individual-based model (IBM) to look at how differences in species movement bias and ability affect species diversity under FPS. FPS is defined and mitigated at a human perspective that may not match a species perspective (Bollmann et al., 2005; Betts et al., 2014; Brodie and Newmark, 2019; Chetcuti et al., 2019). Using an IBM, I can apply the human-defined FPS, typical of considering the fragmentation of a land cover, while allowing for the species level perspective, which results in different movement and mortality in different matrix land covers.

To address the first hypothesis, I simulated different times spent in the matrix by using a biased movement towards more suitable land cover with higher bias corresponding to less time in the matrix. Increasing bias causes individuals to choose more suitable land covers when they are close to a land cover, therefore, to address the second hypothesis, I simulated different patch encounter rates by changing how the species move, from RW, through HDW to CRW. RW species have a low ability to move across the landscape, HDW species can be parameterised to move more directionally in the matrix and CRW species move directionally in both matrix and suitable land cover turning little and therefore constantly move across the landscape. The HDW and CRW species, do not move towards a new patch, but because they are passing through the landscape more, in general they encounter more patches of habitat. I hope to bring clarity to the debate that has arisen over whether FPS has a positive or negative effect on species-diversity (Fahrig, 2017; Fletcher et al., 2018; Fahrig, 2019; Fahrig et al., 2019; Thompson et al., 2019). Specifically, I consider if the differences could depend on the species studied (De Camargo et al., 2018; Valente and Betts, 2019) leading, therefore, to more complicated outcomes than FPS simply having a negative or positive effect on species diversity (Thompson et al., 2019).

6.3 Methods

My multi-species and landscape-scale simulation (Figure 6-1) was built using the 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 has been described following the ***O****verview,* ***D****esign concepts,* ***D****etails* (ODD) protocol for describing individual- and agent-based models (Grimm et al., 2006; Grimm et al., 2010). To aid the readability of these Methods, the ODD is in chapter 3.

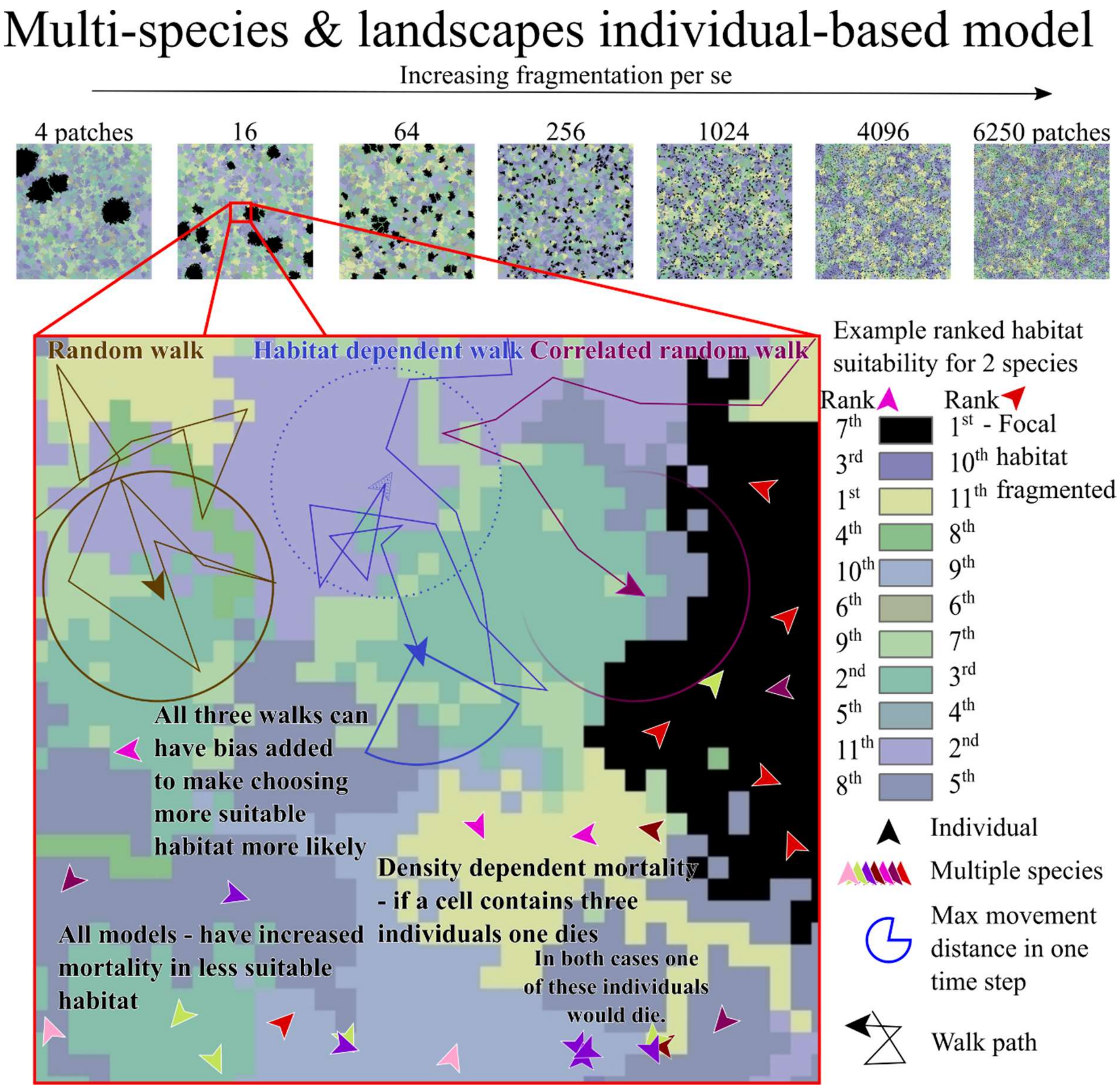


Figure 6-1 A figurative description of the individual-based model, showing how I represented FPS by increasing the number of patches of the focal habitat (in black) while keeping its total area the same. I give two examples of the ranked suitability for land covers on the right for a non-focal-habitat species on the left and a focal-species on the right. I used three different kinds of walk, random walk (RW), correlated random walk (CRW) and habitat dependent walk (HDW). I included more variation is walks by modifying the rate of individuals' transition to a more directed walk within the HDW. All individuals interact with the land covers according to their assigned suitability, with habitat-modified mortality. I varied bias in choosing land cover to make choosing more suitable land cover more likely. These biases ranged between no bias (zero) and high bias (two).

6.3.1 Land cover generation

I did not use real land cover data in this study. Instead I opted to generate land covers. In real land cover data with different levels 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, I simulated land covers over which I had precise control by using the technique described in chapter 4. FPS was represented by the number of patches, with more fragmented landscapes having more patches of focal-habitat (Figure 6-1). 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 Chapter 4 showed the same effects of FPS for when the focal-habitat had 10% or 40% cover. The matrix land covers between focal-habitat patches contained ten different land covers. The number of patches of each of the matrix land covers varied for all but the last generated, chosen from a uniform distribution between 1 and 200 patches for each. The area of each land cover was also randomly generated to be a proportion of the available space in the matrix. The last land cover generated filled all remaining space and could, because it included the space between patches more often include linear features and could have any number of patches. The matrix land covers were generated in a random order so that the last generated was not always the same land cover type. Each focal-habitat and matrix land cover patch (except the last generated), were randomly located within the landscape, but at least two cells apart. Each patch was then grown until the land cover covered the specified area while still remaining separate from another patch of the same land cover by at least two cells. For the matrix land covers, if a land cover could be grown no further, that land cover was considered finished and the next land cover was grown. The land-covers generated for the simulations were 1000 × 1000 cells in size.

6.3.2 Species

The species in this simulation were specified in a similar way to those in the two previous chapters, chapters 4 and 5. All individuals of all species reproduce, generating an additional individual with a probability of 5×10^{-4} during a time step, and can move up to a maximum of 5 cells from their current location. These values were arbitrary but approximate real species at different scales. For example, based on allometric equations (Sibly et al., 2013) this could be, 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. A maximum of two individuals can coexist in a single cell; all additional individuals die (Figure 6-1). The simulation iterated through individuals in random order so that the simulation did not always assess the same individuals first within each time-step. 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. To simulate density-dependent mortality, if an individual counted more than two individuals were in the same cell, it died. There is an overall carrying capacity of 4000 individuals. Above this, an individual had a slightly higher probability of dying within a time step.

Each species has a rank for the eleven land covers in the land cover specifying how suitable that species finds each land cover. These ranks are randomly assigned to each of the species. All species have increased mortality in less suitable land cover. This increased mortality is the same as for the habitat dependency scenario of chapter 4 and all scenarios in chapter 5. This additional habitat mortality is specified by using a logistic equation to relate the rank for land covers to a multiplying value between zero and one. These values were multiplied by the overall rate of reproduction, to give a similar order of magnitude value to reproduction, to give an additional probability of dying within a time step (Figure 6-2). This multiplication meant the highest additional mortality equaled the reproduction probability.

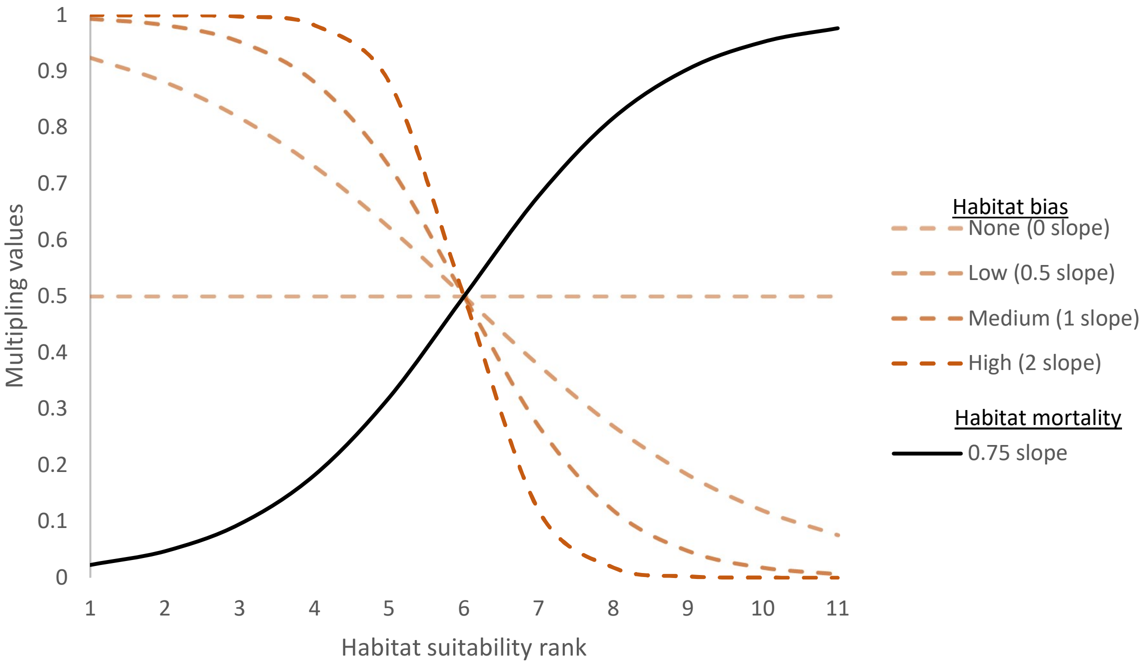


Figure 6-2 Showing how the logistic equations were used to relate the habitat suitability rank, one to eleven, to both increased habitat mortality in less suitable and bias towards more suitable land cover. The same additional mortality slope was used for all species in all scenarios. Habitat bias was varied from none to high bias. The multiplying values were multiplied by the reproductive rate to give additional mortality that was of a similar magnitude to reproduction and in the case of bias used to modify the probability of choosing a more suitable land cover.

In this chapter I only focus on the focal-habitat-species. I define focal-habitat-species as those species for whom the focal-habitat is most suitable (habitat suitability rank one). To test the effects of focal-habitat-species spending more time in the matrix land covers and the species being able to move between patches more readily, 24 scenarios were run. The 24 scenarios were run with different habitat biases (Figure 6-2) and walk types (Figure 6-1). The habitat bias was represented by logistic curves that converted the habitat suitability rank to a value between zero and one (Figure 6-2). I used four different levels of bias, none, low, medium and high. These values between zero and one were then converted to a probability which is used along with the area of each land cover into which the species could move. This bias results in an increase in the probability of a species choosing to move into a more suitable land cover. I used six different walks, a random walk (RW), correlated-random walk (CRW) and four habitat dependent walks (HDWs). When bias is zero, they are RW, CRW and HDWs, but technically when bias is greater than zero, then they should be biased-random-walk, biased-correlated-random walk and biased-habitat dependent walk, for simplicity and comparability I refer to them as RW, CRW and HDW with or without bias. The RW individuals can move in any direction up to the maximum 5 cells movement distance. The CRW individuals can turn within an angle centred on where they are currently facing, which is defined by a gamma distribution of alpha=1 lambda=2 multiplied by 3600, giving a median turn of 36° but the ability to turn through big angles occasionally. This angle defines a sector the individual could move into up to the maximum 5 cells movement distance. The HDW walk is defined by a negative exponential function that relates the habitat suitability rank of an individual of a species to a turning angle (Figure 6-3). The four HDW walks have exponents of 0.1, 0.25, 0.5 and 1, which give walks that deviate progressively more from an RW, with movement in the least suitable land cover eventually becoming like a CRW, but always remaining an RW in suitable land cover. RW species do not move directly through the landscape. HDW walks with progressively higher exponents move more directly across the matrix between patches. CRW always move directly across both the matrix and patches of suitable land cover. HDW individuals have the best of both RW and CRW, able to turn readily with an RW within suitable land cover patches but traverse less suitable land cover like the CRW. I did not use a lag in changing walk mode for the HDW.

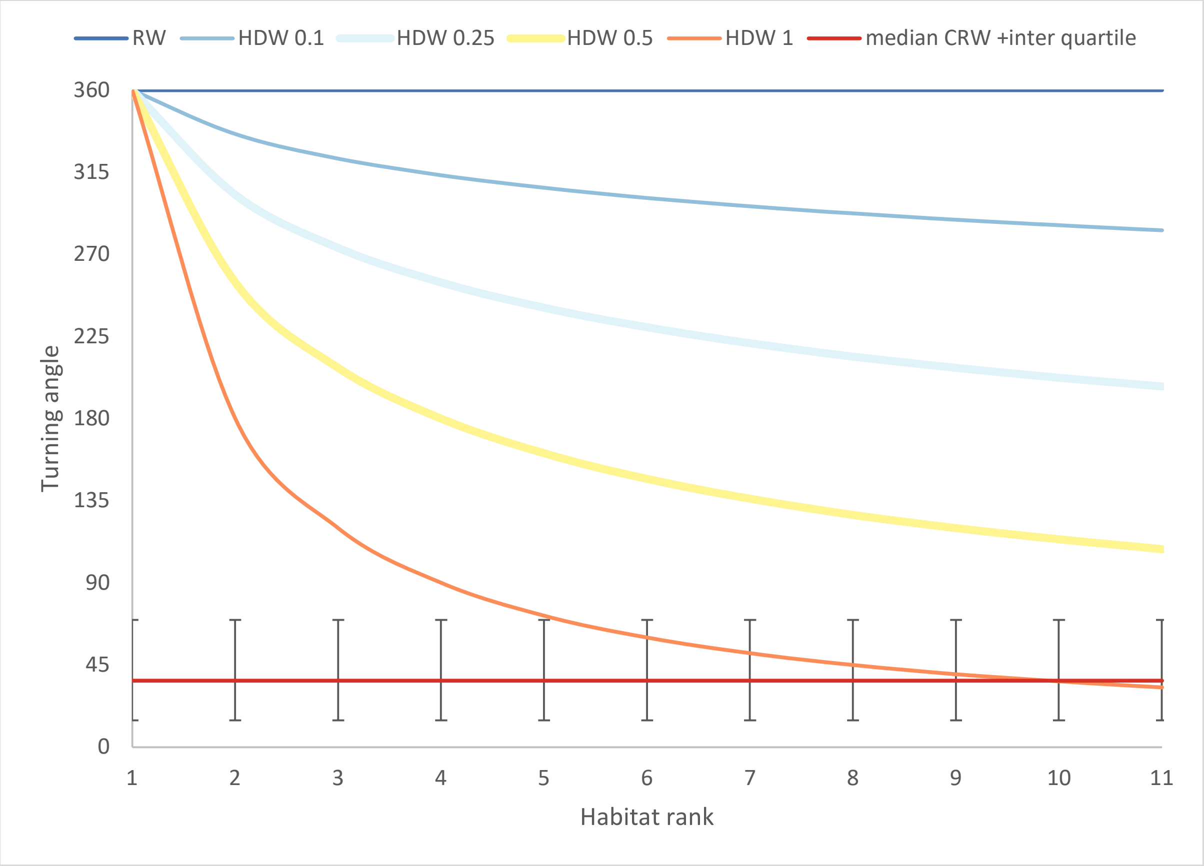


Figure 6-3 Showing how the angle defining where the species can move to (turning angle) changes with the ranked habitat suitability of the species for the habitat dependent walk (HDW) compared to the random walk (RW) and correlated random walk (CRW). RW species can turn completely around. CRW species 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 sharper turning angles. The HDW species can turn completely around in suitable land cover like the RW species, and move more directly in less suitable land cover.

6.3.3 Multi-species and landscapes model description

The simulation loaded the land cover data and ten individuals of each of 400 species. Each individual had a random starting location within the 1000 × 1000 cell simulations. The simulation is toroidal, as in chapter 5, meaning individuals who pass out of one edge reappear on the other side of the landscape. By using a toroidal design, I assumed the landscape to be in a wider landscape that is the same as the landscape of the simulation. To minimize individuals with bias turning away or choosing to cross over the boundary to avoid or gain access to land cover on the other side of the simulation, an additional 10 cells width strip was added around the edge of the 1000 × 1000 cells of the land cover. Each cell in this strip was randomly assigned a different land cover. This randomized the individuals passing from one side of the simulation to the other. The simulation was run for 200,000 time-steps. Using a high number of time steps allowed the number of species to reduce within the simulation to close to an asymptotic number of species. At the end of the simulations, the patch and species of every individual in the focal-habitat was recorded. Each species movement type and level of FPS was repeated 50 times. This resulted in 8398 simulation runs (two runs failed).

6.3.4 Alpha, beta and gamma-diversity

Using the information on focal-habitat-species in each patch, mean patch alpha-diversity, mean pairwise patch (i.e. between pairs of patches) beta sim diversity (Barwell et al., 2015) and overall gamma-diversity of the focal-habitat were calculated using the R package ‘vegan’ (Oksanen et al., 2019). As I did in chapter 5, I focused exclusively on the species for whom the focal-habitat was most suitable (focal-habitat-species) as they were most dependent on the focal-habitat and therefore most strongly affected by increasing the FPS of their habitat.

6.3.5 Analysis of results

I analyzed the results by constructing generalised 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 patches, which represented FPS. I then graphed these trend lines. Due to the simulation nature of my study, using p-values is not advisable (White et al., 2014). I instead focus on effect size and 95% confidence intervals. The effect size is usually over an increase of a unit of the independent variable. In my study this would be a patch but this is meaningless. It is more appropriate to consider the effect size over the range of FPS simulated. I calculated the effects over the range of FPS using the R package ‘effects’ (Fox, 2003; Fox and Weisberg, 2019). This approach is similar to that of chapter 4 and 5. To aid in communication, each of the scenarios has been labelled a to d increasing in bias and 1 to 6 going from a random walk to a progressively more corelated walk (Table 6-1).

Table 6-1 Alphabetical labeling of each species group, defined by varying bias towards more suitable land cover and the walk of the species. The species move with a random walk (RW), habitat dependent walk (HDW) and correlated random walk (CRW). The HDW species, move more like a RW in the matrix with a coefficient of 0.1, and more like a CRW with a coefficient of 1. See Figure 6-3 for further explanation of the walks.

Bias none (0)	Bias low (0.5)	Bias medium (1)	Bias high (2)	
a1	b1	c1	d1	RW
a2	b2	c2	d2	HDW 0.1
a3	b3	c3	d3	HDW 0.25
a4	b4	c4	d4	HDW 0.5
a5	b5	c5	d5	HDW 1
a6	b6	c6	d6	CRW

6.4 Results

To show how alpha-, beta- and gamma-diversity change with FPS and with the different walks and bias, the results are displayed in a multi panel graph, which is first explained in *Figure 6-4* and then presented in Figure 6-5.

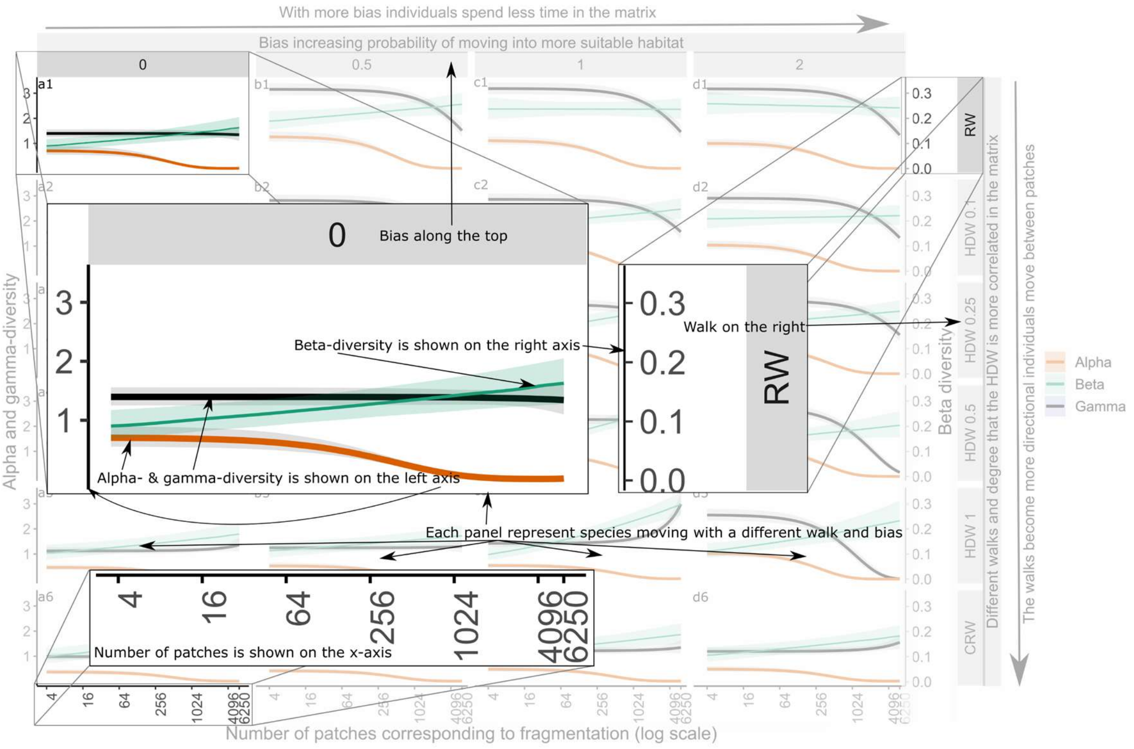


Figure 6-4 Explanation of graph Figure 6-5. Each panel shows a different walk and bias set up. Alpha- and gamma-diversity are both count data and are shown on the left axis. Because beta-diversity only varies between zero and one, beta-diversity is shown on the right axis. To identify what each panel represents, look at the bias along the top grey bar and the walk on the righ grey bar. The axis for alpha- and gamma-diversity, beta-diversity and the number of patches are repeated for each row and colum.With no bias the focal-habitat-species gamma-diversities across the different scenarios and different walks were unaffected by FPS, looking at effect size, changing by -0.04, -0.47, -0.11, -0.10, 0.23 and 0.09 species over the full range of FPS (Figure 6-5 a), despite the fact that the species would have experienced increased mortality in less

suitable land cover. Alpha-diversity decreased less with a more directional walk across the total range of FPS, from RW through the HDW scenarios to CRW (-2.22 to -0.84 species). Beta diversity increased overall, but not by a large amount (0.08, 0.06, 0.07, 0.07, 0.08 and 0.11). The alpha and beta-diversity of the focal-habitat-species almost completely balanced each other, explaining the limited change in gamma-diversity.

Increasing the bias of individuals in moving towards more suitable land cover led to cases where FPS affected gamma-diversity (Figure 6-5). With increased bias, the gamma-diversity of species 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. Alpha-diversity always decreased (by between -0.84 and -3.39), while 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%).

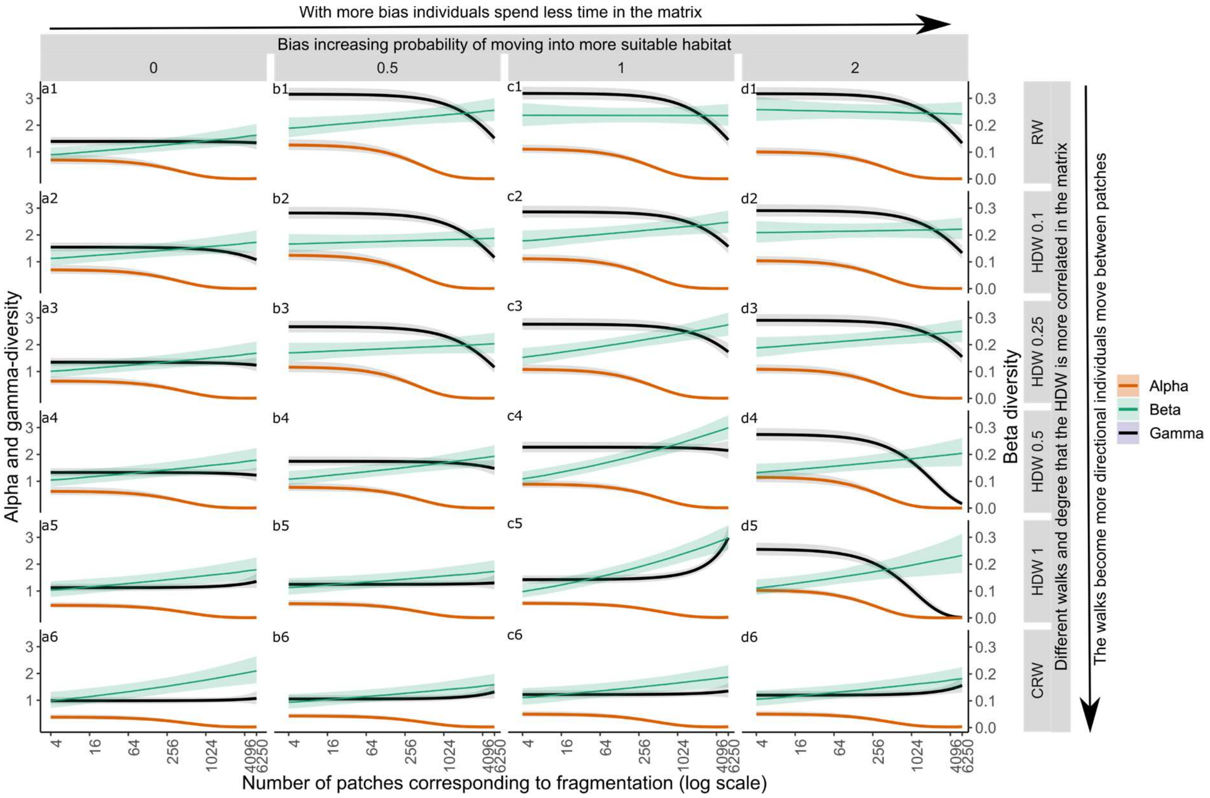


Figure 6-5 Alpha-diversity declining in orange, beta-diversity increasing in green and gamma-diversity both increasing and declining in black with FPS for the different scenarios. SE shown as area either side of lines.

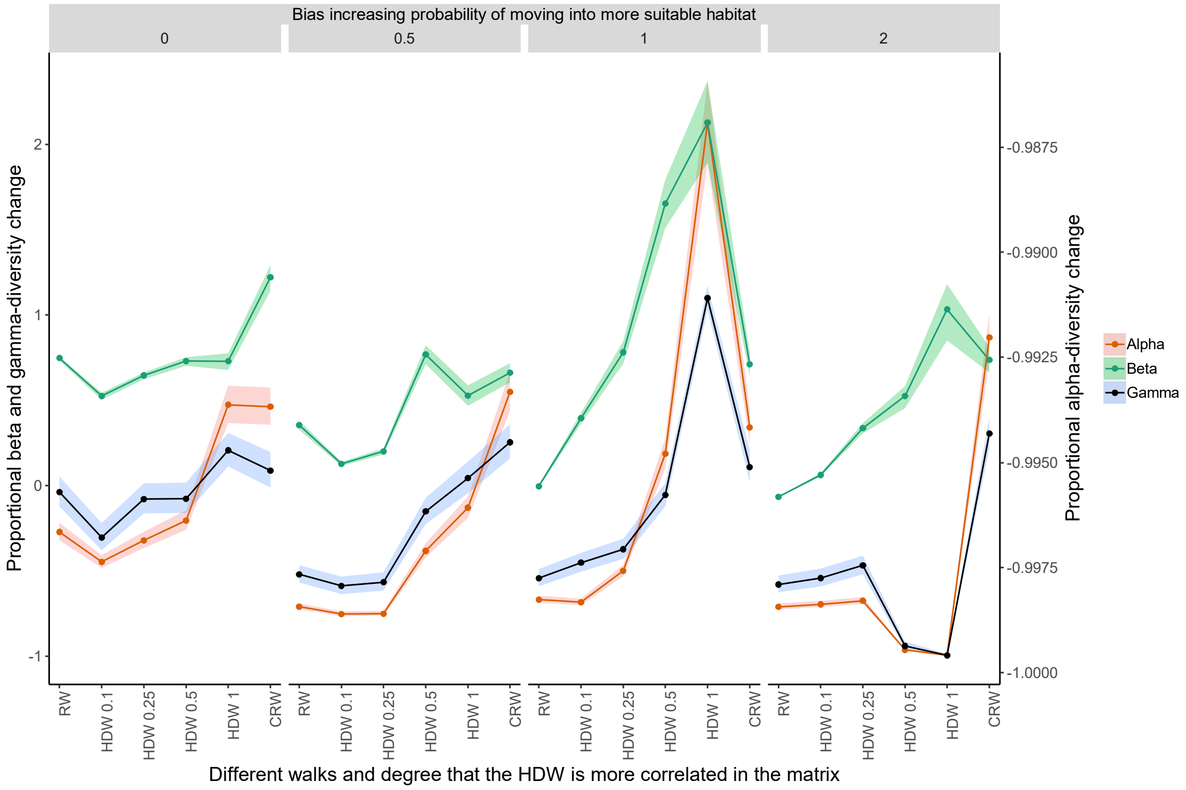


Figure 6-6 The proportional change in alpha, beta and gamma-diversity of the focal-habitat-species over the full range of FPS (4 patches to 6350 patches). Beta and gamma-diversity are on the left axis, alpha-diversity is on the right axis as the proportional change is large and negative.

With bias, the gamma-diversity of RW species always declined with increasing FPS, as they are unable to pass readily between patches of the focal-habitat (Figure 6-5 b1 -1.64, c1 -1.73, and d1 -1.84). With bias, the 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), but very similar when comparing the different levels of biases. With increasing bias, the gamma-diversity declined more, due to the beta-diversity declining (b1 0.07, c1 -0.00 and d1 -0.02) even though alpha-diversity decreased less (Figure 6-6). The lesser decrease in alpha-diversity was probably due to fewer individuals leaving the focal-habitat with higher bias and therefore their risk of mortality is lower and fewer species are lost. With more species surviving in the focal-habitat, the patches share more species and the beta-diversity with FPS decreases with higher bias, further reducing the alpha-diversity loss and gamma-diversity decreases more. The gamma-diversity with at the highest number of 6250 patches, was very similar across the different levels of bias (a1 1.34, b1 1.51, c1 1.45, d1 1.33).

Gamma-diversity of CRW species who turned infrequently and, therefore, had the ability to traverse the landscape rapidly, increased with FPS, although only by a very small amount (Figure 6-5, b6 +0.27,c6w +0.13 and d6 +0.36). Increasing bias affected alpha (-0.89, -1.19 and -1.05), beta (+0.07, +0.08 and +0.08) and gamma-diversity very little. This very low increase in gamma-diversity with FPS for the CRW species is due to the inability of individuals to stay within the focal-habitat patches having encountered them. The CRW species encounter 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.

I looked at four variations of the HDW species by varying the exponent of the negative exponential relationship from 0.1 to one. With the 0.1 exponents, the individuals of the focal-habitat species turn more in the matrix and with an exponent of one they turn little (Figure 6-3). 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 with changing bias (Figure 6-6). As the HDW became more directional in less suitable land cover (with higher exponents), for low and moderate bias, the relationship of gamma-diversity to FPS changed from negative (b2 -1.66 and c2 -1.29), to positive (Figure 6-5 b5 +0.05 and c5 +1.56). The increase with low bias (b5) was very small but larger with moderate bias (c5). The alpha-diversity decreased less with a more directional walk than a more RW for both low (b2 -3.24 most RW like HDW,b3j -2.90, b4 -1.98 and b5 -1.40 most directional HDW) and moderate bias (c2-2.64 most RW like HDW, c3 -2.48, c4 -2.03 & c5-1.24 most directional HDW). Beta-diversity increased with the more directed walks (b2 +0.02 to b5 +0.06, and c2 +0.06 to c5 +0.20). This change with more direct walks was very small with low bias (b2 – b5) but changed by a larger amount with moderate bias (c2 – c5). 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. The positive changes in beta- and gamma-diversity, and lower decreases in alpha-diversity with more direct walks support the idea of increasing functional connectivity. 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.

In contrast to the changing relationship of gamma-diversity to FPS from negative to positive with more direct walks with moderate bias (c2 to c5), having high 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 land cover. They would therefore leave patches of habitat rarely. Gamma-diversity declined more with more directional walks (Figure 6-5 d2 -1.58, d3 -1.36, d4 -2.58 and d5 -2.54). The decline in gamma-diversity with FPS, changed by a large amount between d3 and d4. Alpha-diversity reduced less, as it had done with the low and moderate bias, but not by as much (from d2 -2.47 to d5t -1.83). Beta-diversity increased less (d2 +0.01 to d5 +0.12), and with the declines in alpha-diversity this explained the declines in gamma-diversity (Figure 6-6). This was because, with high bias, individuals rarely leave patches of focal-habitat. Although if individuals did leave they would be able to move across the landscape easily, because they did not leave the effect was the same as if the landscape had low connectivity, with species not moving between patches and having lower alpha-diversity and a smaller increase in beta-diversity.

In general, alpha-diversity decreased less with a more directed walk, from an RW through the HDW to CRW. Gamma-diversity decreased less, except under the highest bias. Figure 6-6, showing the proportional change in alpha, beta, and gamma-diversity, shows the strong influence alpha-diversity had on gamma-diversity. Gamma-diversity always followed alpha-diversity, but this was modified by beta-diversity patterns.

6.5 Discussion

My results show that spending less time in the matrix through having a high bias and therefore high patch fidelity, can be beneficial to species that are able to move across the less suitable land covers. Critically, too high a bias and therefore high patch fidelity or low likelihood of leaving a patch can cause alpha- and gamma-diversity of species that could 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 bias, as might be the case with passive dispersers, such as seeds or some insects, FPS had no effect in my study. My 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 (Haddad et al., 2015; Fletcher et al., 2018), 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 land cover diversity and competitive release causing beta-diversity to increase strongly.

Calls for additional landscape-scale analysis (Fahrig, 2017; Fahrig, 2019; Fahrig et al., 2019) are relevant and these studies are needed. But, 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 land cover, as I 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 looking at the effect of FPS on the diversity of multiple species, there are examples of studies looking at individual species, of species moving with a random walk and being negatively affected by fragmentation, as in the case of an endangered ground beetle which rarely moves with a directed walk, but rather usually moves with a biased random walk (Bérces and Růžičková, 2019). Likewise, there are cases of a species moving more directly and appearing to be unaffected by fragmentation, as in the case of pandas that showed no genetic differentiation caused by fragmentation (Ma et al., 2018). 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, hypothesising that species would move in a similar way to my HDW. They instead found the birds turned more randomly, often switching direction sharply, and the authors suggested that the starlings may have adapted to fragmentation through behavioural plasticity. A mode of movement that I have not included, but which may have different effects, are foray loops, which is being found in 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 I 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.

By using 400 starting species and by generating them randomly anew in each simulation run, it is not possible to determine whether individual species persist with increased FPS. Due to the random nature of the matrix and associated species, there is no reason to assume that particular species would consistently do better with FPS and therefore replace ones from un-fragmented landscapes, as my landscapes did not include species with different walks in any particular run. If I had run the fragmented landscapes in a series of increasing FPS with only those surviving in the last level of FPS, then gamma-diversity could only have either remained constant or declined as no more species could enter the landscape. Assuming other species arriving from surrounding landscapes (introduced at the edge and not just through the toroidal landscape) may have negated the effort of running the fragmented landscapes in a series of increasing FPS with only those surviving in the last level of FPS, as the all of the initial species could be introduced at the edge. This could lead to a slightly different result if the numbers of individuals entering at the edge of the scenario meant some of the species could not establish themselves in a particular level of FPS. Although this again would lead to gamma-diversity increasing less with FPS. This logic does have implications for my results, however. It implies that in a wider landscape with a reduction of species diversity, the outcome of increasing species diversity with FPS would be less likely.

My study did not sweep the full range of possible values for each parameter and did not use specific species, but still found both negative and positive effects of FPS on gamma-diversity. My results show that it is possible to get different effects of FPS as a result of simulating distinct species types. The next step should be to investigate how common these different sorts of species are in real landscapes. Are species more able to move between patches and to have moderate fidelity levels in landscapes or habitats that are historically fragmented? Are species with passive dispersal unaffected by FPS, or would they be affected if I had used higher habitat dependent mortality? Further simulations could test this by focusing on species without habitat bias and sweeping a greater range of mortalities. This could be done possibly by 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 land covers. Can species adapt to fragmented landscapes by reducing site fidelity, possibly by becoming bolder through plasticity (Villegas-Ríos et al., 2018)? Another possibility for species to cope with FPS is by becoming better dispersers by an increase in 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).

In conclusion, I show the circumstances that could explain the different results 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 effective connectivity will differ with different sorts of species. As I 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 in to conserve many small patches in other areas. This will give a diversity of different landscape configurations and therefore species across the landscape. The exception to this would be where habitat has historically only been found in large contiguous areas as species adapted to FPS would be unlikely.

Chapter 7

General discussion

In this thesis I have focussed on the heated debate about whether fragmentation has a universally negative, neutral or positive effect on species diversity (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019). Specifically, I focused on *fragmentation per se* (FPS), which is fragmentation in the absence of, or when controlling for, habitat loss. Patch-scale studies cannot look at the interplay between beta-diversity and alpha-diversity across patches and therefore the overall effects of FPS on gamma-diversity (Mori et al., 2018). As such the extrapolation to a landscape-scale of the results and conclusions from patch-scale studies has been questioned (Fahrig, 2017; Fahrig et al., 2019). I chose, therefore, to study FPS at a landscape scale. Due to the difficulties in conducting this sort of analysis in the field in terms of time, money, and availability of sites and the difficulty of looking at fragmentation while controlling for the area, it is valuable to look at FPS by using a modelling approach. I did this by creating an *individual-based model* (IBM), in which I could simulate multiple generic species, species that are designed to have general characteristics to allow for exploration of ecological principles (Jepsen et al., 2005), and simulate land covers with FPS represented by varying the number of focal-habitats patches. Within the IBM, species could move and interact with the land covers. I then used this IBM, different generic species, and the simulated land covers to test hypotheses concerning circumstances which could lead to negative, neutral, or positive effects of FPS on gamma-diversity. I also looked at the effects of FPS on alpha- and beta-diversity to explain why in any situation gamma-diversity responded as it did. To assess species diversity responses to FPS, my IBM had to allow multiple species to co-exist within a landscape. One of the ways species coexist within a landscape is through the occupation of different niches (Chesson, 2000). As such, in chapter 2 I explored, using empirical data, how species each have different associations with multiple land cover types. Within my IBM the definition of habitat is different for each species based on this species-level perspective (Betts et al., 2014).

Within the IBM, generic species could experience differing mortality and behaviour in different land covers based on the different associations derived in chapter 2. This allowed species to live in and move through multiple matrix land covers, the land covers between the fragmented focal-habitat patches in my simulation. Chapters 4, 5 and 6 then used this IBM to explore how differences in species specialism, movements through and interactions with the matrix depending on matrix characteristics could cause FPS to have different effects on alpha-, beta-, and gamma-diversity. In chapter 2, I found that no two of the ground beetle (Carabidae) species that I analysed in my case study shared even the same ranked order of association with the 21 different land covers, let alone precisely the same strength of association. As this was a large-scale analysis, covering Great Britain, I looked at the species associations at the level of land cover classes, and did not split these land cover units by different abiotic characteristics, or group them. Analysing more alternatives could have led to a loss of power and this level of association with land cover types is typical of similar types of work on habitat association (Eyre and Luff, 2004; Redhead et al., 2016). Grouping and splitting other land covers or habitats would have been possible but would make more sense in the context of a study that needed this level of detail to answer a particular question. The land cover scale of the analysis allowed for validation of the improvement my method offered. My method was an improvement over other methods (Eyre and Luff, 2004; De Cáceres and Legendre, 2009; Redhead et al., 2016) due to its ability to include more data and deal with species with few records and spatial uncertainty, both from sampling and species movement. This analysis clarified the definition of what I consider to be habitat association, looking at the preference of a species for several land covers, as opposed to species distribution models, predicting where species are likely to be found within a landscape (De Lima et al., 2016), and indicator species analysis which identifies the species which best represent a habitat (Hill et al., 1975; De Gasperis et al., 2016). My definition is congruent with the concept of a species-level perspective of the landscape (Betts et al., 2014). This has implications for fragmentation and connectivity analysis, in that the habitats that are fragmented or made more or less connected likely do not correspond to a single meta-population (Valente and Betts, 2019) or meta-community. Instead, the "habitat" that has or could become fragmented, is defined at the human perspective of conversion, reconfiguration, and conservation. Researchers can then look at the effects that FPS has on the different species who have some dependency on these land cover types. Going forward, I defined the habitat that I fragmented as the focal-habitat. This focal-habitat represented this human perspective, and then each of my generic species had differing suitability and preference for this and the other land covers in-between patches of this focal-habitat, the matrix land covers.

Chapter 4 was my first investigation of the effects of FPS. I included three models in this chapter. The first two were the baseline and habitat-dependency models. The baseline model had species moving over the landscape and among patches, but not interacting with the land covers. The habitat dependency model had individuals who had a bias to move towards more suitable land cover and higher mortality in less suitable land cover. In the baseline model, FPS did not affect gamma-diversity as changes in alpha- and beta-diversity counteracted each other quite closely. This simulation did not sort the species in the landscape, and the species spread randomly through the landscape. When land covers had different suitabilities for distinct species and species showed increased mortality in less suitable land cover and bias towards more suitable land cover, overall the gamma-diversity of the focal-habitat increased with FPS. This increase, however, comprised all species, including species who do less well in the focal-habitat, tourist species, which are seeking suitable land cover and become lost (Alderman et al., 2011) and also those that are just passing through (Eversham and Telfer, 1994; Magurran, 2004). To account for the relationships of species to the focal-habitat, I looked at the species in three groups: those for whom the focal-habitat had low, moderate, or high suitability. The species in the low and moderate group increased in gamma-diversity with FPS. The species most dependent on the focal-habitat, in the high group, declined in diversity with FPS. This supports the call and need, to look at the identity of species in studies of FPS (Fletcher et al., 2018), and not simply state that fragmentation causes either no effect or has a positive effect on diversity without establishing what species are included within the analyses (Fahrig, 2017).

Additionally, it has been suggested that cases where diversity has increased with FPS may be because specialist species increased with FPS, contradicting the idea that only generalists increase in diversity with FPS (Fahrig, 2017). Therefore, in chapter 4 I also included a third model. This specialism model included specialist and generalists, defined by differences in competitiveness of species across land covers. The specialists were more competitive than generalists in land covers they found to be most suitable, but less competitive in land covers they found less suitable. In this scenario, overall gamma-diversity increased, primarily driven by the species in the low and moderate groups who found the focal-habitat less suitable. However, for the species most dependent on the focal-habitat, the high group, FPS no longer had a negative effect, with gamma-diversity not declining. The question then was, did the specialist or generalist species cause this increase? Looking at specialists and generalists separately, neither group declined with FPS. I would have expected one of them to increase while the other declined, especially as with neither specialists nor generalists the species dependent on the focal-habitat declined. The specialists are more and the generalists less competitive than the species in the model with neither specialists nor generalists. However, by creating specialist and generalist species, both species groups were more able to cope with FPS. The specialists were able to cope because they could compete successfully against species less suited to the focal-habitat that encroached into the focal-habitat. The tourists did increase less with FPS in the model with specialists and generalists. The generalists as well seemed to have been more resilient, able to use more of the landscape and competing less with the specialists, suggesting some form of niche separation. Another possibility is that these generalists acted more like the species in the baseline model that had no interaction of species with the land covers or like the species in chapter 6 who had no bias and therefore in both cases no or limited sorting of species into areas of land cover. In both cases, FPS did not affect gamma-diversity. I think this is unlikely in reality, however, because although species sorting in the landscape was lower, the species were not extremely strong generalists and the difference between suitable and unsuitable land cover was still quite high for these generalists. Of course, it is unlikely that species would ever fall into such binary classifications of specialists and generalists, where all species in every other land cover are similarly binary. However, this was at least evidence that different sorts of species can be unaffected by FPS. The overall increase in gamma-diversity also explained why studies may report increases in gamma-diversity when not accounting for species (Fahrig, 2017).

In my first foray into considering FPS, I had jumped straight into looking at landscapes with multiple matrix land covers, influenced by chapter 2 in which I studied habitat associations and the concept of a species-level perspective (Betts et al., 2014). However, many connectivity and fragmentation studies at both patch and landscape-scales, in both empirical and modelling studies, often use binary landscapes with a focal-habitat and a single dissimilar matrix land cover. This is a sensible approach when testing to see if there is any effect. Picking an extreme is likely to produce results and also these extreme landscapes represent a worst-case scenario of landscape conversion of good quality natural habitat surrounded by a desert of poor quality land use, such as arable agriculture or forest plantations (Tscharntke et al., 2012; Haddad et al., 2017; Damschen et al., 2019). This also fits well with island biogeography, with the matrix in this cases being water and therefore for many land species entirely dissimilar (Tscharntke et al., 2012). In these examples, populations of species will strongly associate to a single land cover, as they are unlikely to be equally adapted to both. In cases where they are equally adapted, researchers would rightly label them as being very strongly a generalist species, and therefore having no difference in suitability. My use of multiple land covers allows a more nuanced assessment of FPS. For example, I expected that beta-diversity would increase with FPS because of the positive mechanisms of increased land cover diversity and positive edge effects (Fahrig et al., 2019). With fewer land covers in the matrix, this would not be possible, and beta-diversity would increase less with FPS. I used species like those of the habitat dependency scenario of chapter 4 in five models in chapter 5. The first of these was a baseline model similar to the habitat dependency scenario of chapter 4 (not chapter 4's baseline). The second and third in the focal/matrix similarity scenario were the dissimilarity and similarity matrix models, with the matrix being less or more similar to the focal-habitat than in the baseline. The fourth and fifth in the matrix diversity scenario were the *starting low diversity* (SLD) matrix and *starting high diversity* (SHD) matrix, with the matrix land covers at the start of the simulations having fewer or more species diversity than the focal-habitat and the baseline. In chapters 5 and 6, I only looked at those species most dependent on the focal-habitat, for whom the focal-habitat had suitability of one. This was different from the high group in chapter 4, as that had consisted of those species for whom the focal-habitat had suitability of one, two or three. I labelled these focal-habitat dependent species as the focal-habitat-species and looked at them because FPS would likely affect them most. The prediction that beta-diversity would increase less with FPS when there were fewer land covers was supported. In fact, beta-diversity decreased with dissimilar matrix land covers irrespective of the number of matrix land covers and in the baseline and SLD models with fewer matrix land covers. With a dissimilar matrix, beta-diversity declined with FPS, and the effect on gamma-diversity was extremely negative. Even in the baseline model with the matrix being neither particularly similar nor dissimilar, the beta-diversity declined under FPS with fewer matrix land covers. With ten matrix land covers, beta-diversity no longer declined with FPS, even increasing a small amount, although not enough to stop gamma-diversity declining, albeit not as severely as with the matrix being dissimilar. Therefore, although it is beneficial to use a binary landscape with highly dissimilar land covers in terms of clarity of species association and specialism, doing so may stack the deck against the positive effects of FPS. These dissimilar binary landscapes would undermine the positive mechanism of FPS, through positive edge effects and increased land cover diversity, and so beta-diversity could not increase. This lends support to the need for landscape-scale analysis, and further suggests that researchers should conduct at least some studies on more varied landscapes. This also reinforces the need to maintain and enhance the quality and diversity of matrix land covers to mitigate effects of FPS (van der Hoek et al., 2015; Neilan et al., 2018). A more permeable matrix is also highlighted as a necessity of making corridors and stepping stones effective in increasing connectivity (Baum et al., 2004).

All the species in my simulations in chapters 4 and 5 moved with a random walk. This meant that the species were not good at moving through the landscape and between patches of focal-habitat (Codling et al., 2008). I had given species the ability, in the latter models of chapter 4 and those in chapter 5, to move more often towards more suitable land covers, but in general, any individual would not move across the landscape and choose new patches instead more often encountering already encountered patches. The species, therefore, most often spread between patches through the species as a whole surviving and diffusing across the landscape. However, it has been suggested that species that spend less time in the matrix and those who have higher encounter rates with focal-habitat patches should be affected less negatively by FPS (Fahrig, 2017). Inherent in these suggestions is the concept that not all species move in the same way, with differences both between and within species (Bonte et al., 2012; Bonte and Bafort, 2019). In chapter 6, I varied the strength of movement bias towards more suitable land cover and changed the way species walked across the landscape. As well as the random walk of chapters 4 and 5, I included a correlated-random walk, with individuals turning infrequently and moving across the landscape, and a habitat-dependent walk in which species random-walked in suitable land cover and moved more directly in less suitable land covers and, therefore, traversed unsuitable land cover arriving at new patches of suitable land cover. Interestingly, without movement bias, and therefore no sorting of species in the landscape, FPS had no effect on gamma-diversity with the levels of habitat dependent mortality I had in all three fragmentation chapters. With bias, the habitat-dependent walk species were, with certain parameterisations, not only unaffected by FPS but did better, increasing in gamma-diversity. This supports the idea of increasing functional connectivity, although of course only for particular species (Fahrig, 2017). This support for functional connectivity further highlights the necessity of understanding that connectivity is a species level perspective. In my results some species were negatively affected by FPS as they move with a biased random walk and therefore do not move between patches. This is how the ground beetle species moves in the empirical movement study Bérces and Růžičková (2019) in which they defined their ground beetle species as being threatened by fragmentation. In my results other species moved more directly and were unaffected by fragmentation. This is a similar results to the empirical study of pandas, there was no genetic support for the isolations of meta-populations caused by fragmentation and the pandas were not restricted by barriers or distance (only topography) (Ma et al., 2018).

Functional connectivity is a species-level perspective on movement through a landscape (Bélisle, 2005). Each species will have a unique perspective as I showed in chapter 2, each finding different land covers to have different suitabilities, and therefore connectivity will be different for every species in each landscape. Connectivity is a useful concept when making predictions about landscape change for single species or related groups of species (Brodie and Newmark, 2019). I would argue though that connectivity measures are less useful with progressively larger groups of species. When looking to make generalisations, FPS is more appropriate as it does not include any assumptions over whether we as researchers think a landscape is more or less connected. Fragmentation is the mechanical loss and splitting of habitat patches and is not species-specific, analogous to structural connectivity (Bélisle, 2005). The impacts of fragmentation, as I have shown, will likely be different for different species. FPS, as already stated, is the component of fragmentation that excludes impacts of changing the area of habitat and reflects only the reconfiguring the patches, primarily through splitting into more patches (Fahrig, 2017). FPS is potentially an unrealistic concept, as fragmentation in the real world generally arises through the anthropogenic conversion of an area of one land cover into another, leading *de facto* to a loss in an area of the first. However, it has been shown that area loss often swamps the effect of FPS, and therefore it is useful to isolate fragmentation from area loss and assess impacts of FPS to determine the effect the fragmentation component has on species diversity (Fahrig, 2003; Watling et al., 2020). An example of this is the *species-fragmented area relationship* which suggests lower gamma-diversity than the species-area relationship caused by FPS, but not accounting for beta-diversity increases (Hanski et al., 2013).

It is vital to document which species are included in measurements of diversity when looking at the effects FPS or other spatial reconfigurations have. Measuring the effect of FPS on an individual species is an indication of the connectivity of the landscape for that species. The effect on a meta-community is, therefore, the sum of effects on each species', plus any interaction between the species. The issue of fragmentation is a complex one with multiple factors influencing whether there is an effect of FPS and if this effect is positive or negative (Thompson et al., 2019). Fahrig (2017) seemed to suggest that, despite finding only a majority of studies they looked at showed either no or positive effects, and not all of the studies, that FPS never has a negative effect. They even went as far as suggesting that the idea that FPS has a widespread negative effect was a zombie idea. Zombie idea is too harsh, but studies should better define the circumstances and scale of the study. They should also acknowledge that if they conducted their study at a patch scale, that there could be no measure of beta-diversity or its potential to counteract any loss in alpha-diversity. The zombie idea was likely an attempt to provoke scientists working on connectivity into admitting that fragmentation does not always have a negative effect. My work does support doubt in the absolutism of two other of the ideas Fahrig (2017) included in the "fragmentation zombie family"; that fragmentation always reduces connectivity and that specialists are particularly affected (although I would never use the term zombie idea, suggesting instead a need for clear definition/documentation). Fragmentation can reduce connectivity (Damschen et al., 2019; Marrotte et al., 2020), but as I and others have shown, it can also increase functional connectivity for certain species (Halstead et al., 2019; Thompson et al., 2019). These species need not necessarily be "generalists", as specialist species with a dispersal phase, adaptation, or bold individuals being able to move to new patches may also experience increased connectivity. Although this may not be the case for all species, only for "Goldilocks species", as Brodie and Newmark (2019, p.752) call them, with a decent quality matrix. Others may still require additional linkages to move around the landscape.

Whether a species is a specialist or generalist is open to interpretation and these classifications are often ill-defined, with studies calling species specialist or generalist idiosyncratically (Da Silveira et al., 2016). Within studies using dissimilar binary landscapes, it is easy to define a specialist species as one that would do poorly in the impoverished matrix and a generalist as one that would do well in either, or even as one that is a specialist of the matrix but uses the edge of the focal-habitat (Da Silveira et al., 2016). I did not design my specialist species to be only associated with a single land cover, but that is how they may have appeared with a simplified landscape. If the landscape had been simpler, we may not have found that the specialists were unaffected by fragmentation, due to the extremely negative response of both beta- and gamma-diversity to both matrix dissimilarity and few matrix land covers. Likewise, the positive response of mobile species, potentially adapted to fragmented landscapes, may be swamped by the lack of an increase in beta-diversity in a binary landscape.

7.1 Limitations and caveats

The size of the simulation, in terms of spatial extent, may have been a limiting factor of my fragmentation analysis. The 1000 × 1000 cell extent of my analysis is not particularly large and the densities of individuals in the landscape are lower than would be the case in the real world. However my 1000 × 1000 cell extent is comparable or larger than similar IBM fragmentation studies (Aben et al., 2014; Rybicki et al., 2019; Hunter-Ayad and Hassall, 2020), if slightly smaller (although of a similar magnitude) than some IBMs generally (Engel et al., 2017). Due to limitations in the processing power and time, it was necessary to add a cap on the number of species and the density of individuals in cells, this limited the strength of the interactions between individuals, something which other IBM models have shown to have no ill effect (Bilde and Topping, 2004). This may not have been a big issue if considering the cell size as meters but may have become less realistic if a cell represented a kilometre. The limited extent is one of the reasons the diversity was low in my simulation and why my effect sizes were low. Another reason the effect sizes were low was the simplicity of the available niches. Including another form of niche differentiator, for example, elevation, and then having each species randomly assigned a range of elevations range would have allowed for more species. I think more species would have strengthened the effect size, both negative and positive, because higher numbers of species have more potential to decline or increase. But this increase in size would not have changed the overall conclusions.

Because real land cover data contain many correlated characteristics (Cushman et al., 2008; Fletcher et al., 2018), I designed the land cover generator to allow me to distribute patches through the landscape regularly, randomly or in a clustered way. I chose to run all analysis with patches randomly distributed within the landscape, as there was no reason to assume FPS called for patches to be either regular or clumped. Even so, my land covers often had clumped patches. This is not a problem, as this is to be expected and this would likely make little difference due to the large steps in the number of patches I used to represent FPS, 2^n (excluding 2) in chapter 4, and 4^n in chapters 5 and 6. Looking at the clusters of patches for example, in the four patches cases, if three were close together there would be two clusters. In the 16 patches case, which is the next step up in number of patches after the four patches case, looking at Figure 5.1 in chapter 5, there were 12 or 13 clusters. This is still very different to four patches case. This likely increased the variation in diversity outcomes at any level of FPS (the number of patches). This again likely made my effect sizes smaller than they might have been. I specified the number of patches and area of the focal-habitat but specified the matrix less strongly. The matrix land covers were not as fragmented as the focal-habitat. I could have co-varied fragmentation of each land cover, but this would have been difficult to create. One reviewer of the paper for chapter 4 suggested I should have looked at the species in each of the other land covers, but I am not sure why this would have been beneficial. I think the simplest option would have been to have a larger range of landscapes by varying the number of patches of each matrix land cover beyond the 200 that I used as the maximum number of patches for each matrix land cover. However, there is no reason to assume a natural land cover that is experiencing FPS would exist in a landscape where all other land covers are also becoming more fragmented. I could have fragmented one or two other matrix land covers in the same way as the focal-habitat. Would fragmenting these other land covers have told us anything new, however? As it is, the last matrix land cover created by the land cover generating process was by default more varied in terms of the number of patches and shape, including linear features.

The simulations were not entirely realistic because when I changed an attribute like specialism, walk, or bias, I did the same to all the species in the landscape and they were all the same. Many IBM studies are conducted on single real species (Jepsen et al., 2005) but those using generic species have similarly had all species sharing many properties (Rybicki et al., 2019). Would it have been better to have most of the species in the landscape be entirely random in terms of specialism, speed, movement, bias and then changing focal-habitat-species to either be all of one type, specialist/generalists for example, or taking randomly created focal-habitat-species and making half more specialist and the other half more generalist? The simulation already contained randomness because of the way I generated species and landscapes. With enough variation in the species in the matrix, the matrix community would potentially end up perfectly adapted to the landscape. This would mean more pressure on the species for whom the focal-habitat is most suitable and make the result of FPS more likely to be negative. However, if humans created several of the land covers in the land covers in the matrix through the conversion of parts of the focal-habitat, it is unlikely the species will be so perfectly adapted to these matrix land covers. It would be a worthwhile experiment to look at the effect of doing the analysis in this way. The reader should treat my simulations as indicative only, and not as proof of FPS being positive or negative in any particular real-world situation. They only show that it is possible, depending on species and landscape characteristics, for FPS to have no effect, a positive, or a negative effect.

I also fixed the perceptual range of the individuals to the maximum movement distance. The perceptual distance is likely further (Thiele, 1977). Fixing these attributes to be the same was computationally expedient. Having two choices, long-distance and within maximum distance, every movement would have required at least two levels of decision; where am I going and what step shall I take now. This could replace the different walks I used, but I would need information on how far species are willing to deviate from a straight course to reach an eventual location. The walks I used are a way to represent observed behaviour, therefore the way I have modelled movement is likely similar to what would emerge with different levels of perception and memory. Aben et al. (2018) advocate the use of viewsheds to differentiate where species can see and to explain sub-optimal movements. For me to have taken this sort of approach would have required topography in our model. Equally, I could have included memory in individuals of previous locations (Grant et al., 2018). But studies have chosen to not include memory when looking at movement, to allow for a focus on the interaction of movement and the environment (Holloway, 2019). My approach is taking these sort of movement analyses and having species interact with the environment, therefore memory would have been a potential over-complication. However, adding in memory could allow for analysis of whether including memory would complicate movement analysis or not. These sorts of approaches could be added in future adaptation to implementing species-specific modelling of the effects of FPS. I also used a simplistic case of density-dependent mortality, with inter- and intra-species density dependence the same. Others have achieved similar density dependence by using common resources, although they split these into different groups of species that use a few different types of resource and therefore had no density dependence between groups (Rybicki et al., 2019). I wrote the simulation to allow me to vary these two types of density dependence separately and differently for different species, doing so would be a move to higher realism than has been included in this simulation.

All these additional parameter sweeps were not possible during my PhD due to a decision I made not to convert my NetLogo simulation to a faster programming language (C++). I had spent a month converting a different IBM from NetLogo to C++ via python and cythonisation which I had based on the ground beetle IBM of Bilde and Topping (2004). Doing so I reduced run time to about 2% of the NetLogo version. Similar gains would have caused my simulation to run in 30 minutes instead of the 24 hours each run took. I instead opted to save the month and instead rely on using high powered computing. With the benefit of hindsight, I might have been able to run more experiments with each run taking 30 minutes. However, the main trends in my results would likely not have changed. These additional parameter sweeps could be run however in further work.

7.2 Further work

In their review of the SLOSS debate, Fahrig (2020) found more support for several small (SS) over single large (SL) habitat patches. Conclusions like specialists having higher diversity with SS, and colonization outweighing patch scale extinction are both supported by the results of my thesis, with specialists being unaffected by FPS and species more able to move between patches being positively affected by FPS. However, Fahrig (2020) also found that SS patches had higher diversity in a more hostile matrix. This is in disagreement with what I show with a more hostile matrix, in my dissimilarity model of chapter 5. Fahrig (2020) suggests that most species can colonise successfully. But I do not use higher dispersing individuals, those with a habitat dependent walk (HDW) (chapter 6), in a hostile matrix (chapter 5). For this reason, further work could include combining some of the scenarios from the different chapters. I would like to see if the focal-habitat-species from chapter 6 who were able to move between patches of focal-habitat with a HDW, leading to an increase in gamma-diversity, would still be able to increase in diversity with the dissimilar matrix land cover. Based on Fahrig (2020) they should still increase in gamma-diversity. Fahrig (2020) also talks about a diversity of land covers and fragmented or SL patches interacting with more land covers. If the gamma-diversity did still increase with mobile species and in a hostile matrix, would this still hold with fewer matrix land covers as I did in chapter 5? I suspect they would not because the beta-diversity would increase less.

I have found different effects of FPS on different generic species, but if reviews of empirical studies on FPS and SLOSS are only finding particular results (Fahrig, 2017; Fletcher et al., 2018; Wintle et al., 2019; Fahrig et al., 2019; Watling et al., 2020; Fahrig, 2020), do only certain sorts of species exist, or because there is not universal agreement on the effects of FPS, is this because they are looking at different species as I have assumed in chapter 6. Future work could involve parameterising an IBM similar to my analysis for real species. I had hoped to try to parameterise the simulation with values for ground beetles, incorporating data from chapter 2, size and allometric speed and reproductive rates. I had then hoped to conduct approximate Bayesian computation (van der Vaart et al., 2016) trying to approximate the habitat association results from chapter 2 using the IBM, and determine differences in the bias towards, mortality and reproductive rate of different land covers for each species. I could also have potentially used different modes of movement. This would have given insights into exactly what the phi-coefficient from chapter 2 represents in terms of preference, mortality, and reproduction. Then, having parameterised the simulation to be as realistic as possible, I could have run analysis to see how these species collectively and in groups reacted to FPS. I originally planned this as the last chapter, but I realised that this could involve as much work and processing as the whole of the PhD as it is now. This would, therefore, be ideal as a future substantial and standalone project.

There is the idea in IBMs of deconstructing complex computational models to analyse their robustness (Grimm and Berger, 2016). My simulation is simplistic and general, looking for reversals in the relationship of diversity to FPS. It is already deconstructed, and the first step towards a more complex model. Adding in real species data would be a move towards more complexity, but could also include greater variability in land covers, potentially including topography and climate and with real data on different landscapes allowing for answering of questions specific to different locations on the sort of scale and complexity of the ALMaSS agent-based modelling system (Topping et al., 2003). These results would be important in terms of repeatedly testing different circumstances that affect FPS but would not immediately be as generalizable. Even with my model being simplistic, it was not always easy to work out why diversity changed in a particular way. Therefore, immediately having a more complex model would have made results difficult to interpret.

I would also have liked to have moved away from FPS, and looked at the impacts of corridors and stepping-stones (Haddad et al., 2014). For example, in Ma et al. (2018) empirical study they did not appear to be seeing genetic differences in populations of pandas, which suggests they were not being affected by fragmentation but were still advocating planning corridors. It would be interesting to determine the threshold for species generally requiring corridors and whether adding them would have the desired effects, including at which point corridors are not sufficient to help isolated species (Doherty and Driscoll, 2017).

Researchers should develop a framework to document all fragmentation studies due to a lack of clarity in the language used in studies (Miller-Rushing et al., 2019) and the complexity of the FPS debate (Thompson et al., 2019). This would involve clearly appraising if the study is of connectivity, isolation, or fragmentation per se, whether it is at a patch or landscape scale and how big an area they cover. They should also clearly define what exactly is measured in terms of the diversity measure and the species included (Miller-Rushing et al., 2019). Additional information should describe the matrix and the similarity of the focal-habitat and matrix land cover. One approach to this could be the measurement of the phi coefficient of association that I presented in chapter 2 for the species that researchers have in their study, based on larger datasets of species presence. This would allow them to classify species as acting as specialists or generalists and as dependent on or a tourist in the focal-habitat. 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). This 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). Further, this sort of analysis could also be a way forward in practical conservation; allowing for determining exactly how species react to different planning options and how capable species are of moving across different land covers. From this analysis, one could then make better estimates of the effect fragmentation would have on the sorts of species that are in landscapes at risk of change or help to mitigate current lacks of connectivity for the species that are identified as likely needing help.

7.3 Impact

Should the results of chapters 4, 5 and 6 be proven to be representative of the sorts of patterns of FPS effect on species diversity, then they have important consequences for practical conservation. Chapter 3 showed that almost all species of carabid were not restricted to a single land cover type. This suggests a more holistic approach should be taken to practical species conservation. Not simply conserving the woodland habitat of a "woodland" species, for example, but taking into consideration the secondary resources of the species. Additionally, in the planning of conservation of a focal species, the other "woodland" species should be considered further using this approach and additional elements of the landscape conserved or enhanced for these species also. In both cases, habitat association analysis could be performed for a suite of species, and the landscape conservation informed by the insights gained.

Chapter 4 combined with the information on the association of different species in chapter 3 suggests that many specialists, those most strongly restricted to a single land cover type, and generalist species, may be unaffected by fragmentation as long as the landscape contains a diversity of land covers. Still others, those of the middling ground, neither particularly specialist nor generalist may respond badly to fragmentation. Considering the identity and what is meant when species are referred to as specialist or generalist and using analysis of habitat association, conservation efforts could be focused on mitigating fragmentation for those species struggling with a fragmented landscape. Further, specialism could be looked at from the emergent perspective of species appearing specialist because of the other species in the landscape or the design of the landscape, further highlighted in chapter 5. In the absence of more competitive species, such as on islands or isolated corners of the landscape specialist species may utilise a broader range of habitats and benefit further from a heterogeneous landscape of resources and land covers.

In chapter 5, I showed the potential impact of typical analysis choices in fragmentation analysis that of using an extremely different fragmented and matrix land cover types in experimental landscapes. These are often a fragmented woodland and different open habitat types, or a fragmented grassland and different woodland types. In an exploration of fragmentation, this suggested that fragmentation analysis should sometimes look at a greater diversity of landscapes when exploring the effect of fragmentation. But from a practical conservation perspective, this shows the importance of maintaining or creating landscapes with a diversity of land covers and resources. It would be easier, and potentially appear more cost-efficient to pump resources into the conservation of important habitats patches in monoculture landscapes and not to focus on the matrix. However, allowing massive single land use withing the matrix without any mitigation would strongly exacerbate the negative effects of fragmentation. As mentioned for chapter 4, it is also likely that framing in such simplistic binary, "good" and "bad" land cover landscapes, that species would appear to be more specialised, when they may function as a more generalist species in a landscape containing a diversity of landcover elements in the matrix between a fragmented landscape. This could lead to the wrong conservation approach though misclassifying species or different sources classifying species specialism differently. It is also possible that species should be considered specialist or generalist in different landscapes.

Chapter 6 showed a difference, in how species move, their site fidelity or potential boldness when moving out of preferred habitat and moving into the matrix. If different species are shown to respond differently to fragmented landscapes by altering how they move, being bolder or having a higher prevalence of dispersal ability within their populations, this could suggest long term adaptation within fragmented landscapes. Conservation could focus some effort on species-level adaptation to landscapes, increasing adapted individuals within populations to further mitigate the effects of fragmentation where it is not possible to physically decrease fragmentation. This is an idea similar to that of developing immunity to things like avian malaria to conserve island bird species. Populations adapting to fragmentation may need help for some time to allow them to develop enough individuals within the species to survive unassisted in fragmented landscapes. However, the negative costs on the fitness of the species of this increased dispersal adaptation should be further explored lest the species become unviable particularly compared to other species.

7.4 Conclusion

In conclusion, I found that it is possible for differences in species movement and behaviour, and choices of experimental landscapes to change if FPS has a negative or positive effect on gamma-diversity. In my modelling, the species more capable of moving through landscapes or that were more competitive were unaffected by or positively affected by FPS. Having an extremely different, low-diversity or degraded matrix between the focal-habitat more often showed negative effects of FPS. This will have the same effects as patch scale studies, with the positive mechanisms of FPS, land cover diversity and positive edge effects being unable to increase beta-diversity and counter the loss in alpha-diversity caused by smaller patches with increase FPS. Patch scales and simple landscapes will also potentially be making specialists and generalists appear to be more so because of the simplicity of the landscapes.

Changing species specialism, habitat association and movement changed the effect that FPS had on species diversity. Given the different effects, it is important that future studies on fragmentation not only state the species or groups of species that are being looked at in their work but also characterise the different species and potentially look at them in separate groups if there is reason to think that fragmentation may affect them differently. Simple landscapes had a stronger negative effect on diversity than more complex or varied landscapes. Going forward both empirical and modelling studies should also include examples of non-binary landscapes, better covering the variation in landscapes in which a fragmented habitat of concern may be situated.

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Appendix for Chapter 2

Appendix C2.1.

Table A C2-1 Words used to translate Luff (2007) *text into LCM2015* (Rowland et al., 2017) *habitats or aggregates of these habitats. The intertidal aggregate is nested within the coastal aggregate, and therefore if the coastal aggregrate was added it overwrote the intertidal. The same applied with heath and moorland. A lone habitat was also superceded by an aggregate containing it.*

Luff words	**LCM classes**
Flooded, flushes, marshy, mires, reed, reedbed, reedbeds or submerged.	Agg. = ("Fen, marsh and swamp"; Freshwater)
Grass, grassland, grasslands, grassy, meadow or meadows.	Agg. = (Acid grassland; Calcareous grassland; Heather grassland; Neutral grassland; Improved grassland)
Pasture or stables.	Agg. = (Arable and horticulture; Improved grassland)
Forest, trees, woods or woodland.	Agg. = (Broadleaf woodland; Coniferous woodland)
Moorland or moors.	Agg. = (Inland rock; Acid grassland; Heather grassland; Heather; Bog)
Intertidal, inter-tidal, littoral, sea, seaweed, tidal or tide	Agg. = (Littoral rock; Littoral sediment; Saltwater; Saltmarsh)
Brownfield, cellars, garden, gardens, suburban or urban.	Agg. = (Suburban; Urban)
Beaches, buildings, cliff, cliffs, coast, coastal, supralittoral, dune, dunes or estuarine.	Agg. = (Supralittoral rock; Supralittoral sediment; Littoral rock; Littoral sediment; Saltwater; Saltmarsh)
Calluna, heath, heather or heaths.	Agg. = (Heather grassland; Heather; Bog)
Fen, marsh or swamp.	"Fen, marsh and swamp"
Acid grassland.	Acid grassland
Arable or horticulture.	Arable and horticulture
Bog or sphagnum.	Bog
Broadleaf woodland, broadleaf, deciduous or oak.	Broadleaf woodland
Calcareous grassland.	Calcareous grassland
Coniferous woodland, conifer, coniferous or plantation.	Coniferous woodland
Freshwater, lake, lakes, ponds, river, riverine, rivers, stream, streams or water.	Freshwater
Heather.	Heather
Heather grassland.	Heather grassland
Improved grassland.	Improved grassland
Inland rock or rock.	Inland rock
Littoral rock.	Littoral rock
Littoral sediment.	Littoral sediment
Neutral grassland.	Neutral grassland
Saltmarsh.	Saltmarsh
Suburban.	Suburban

Supralittoral rock.	Supralittoral rock
Supralittoral sediment.	Supralittoral sediment
Urban.	Urban

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Appendix C2.2. Most abundant habitat analysis

In the main analysis within this paper we elected to discard all locations which had multiple habitats when conducting the original unweighted analysis. An alternative to this is to choose the most abundant habitat at any location as the habitat of that location.

A C2.2.1. Methods

The methodology was identical to that in the main paper, except that no locations were removed. The weighted and unweighted versions thus had the same number of records for each species. We again calculated both the original chosen habitat and the uncertainty-weighted correlation index ϕ values and permutated (De Cáceres and Legendre, 2009) to get a *p*-value for each habitat and for each carabid species.

A C2.2.2. Results

The unweighted chosen habitat analysis identified on average 62% of Luff habitats and the weighted group equalised analysis 70% both using 239 species. In contrast the unweighted excluding locations analysis conducted in the main paper identified on average 68% of Luff habitats. The chosen habitat analysis also consistently performed worse than the weighted analysis regardless of the number of records (Fig. A C2.0-1) in contrast to Figure 2-1 in the main paper where the unweighted analysis sometimes appeared to match better on average. The chosen habitat analysis however was able to classify all habitat in the same way to the weighted version.

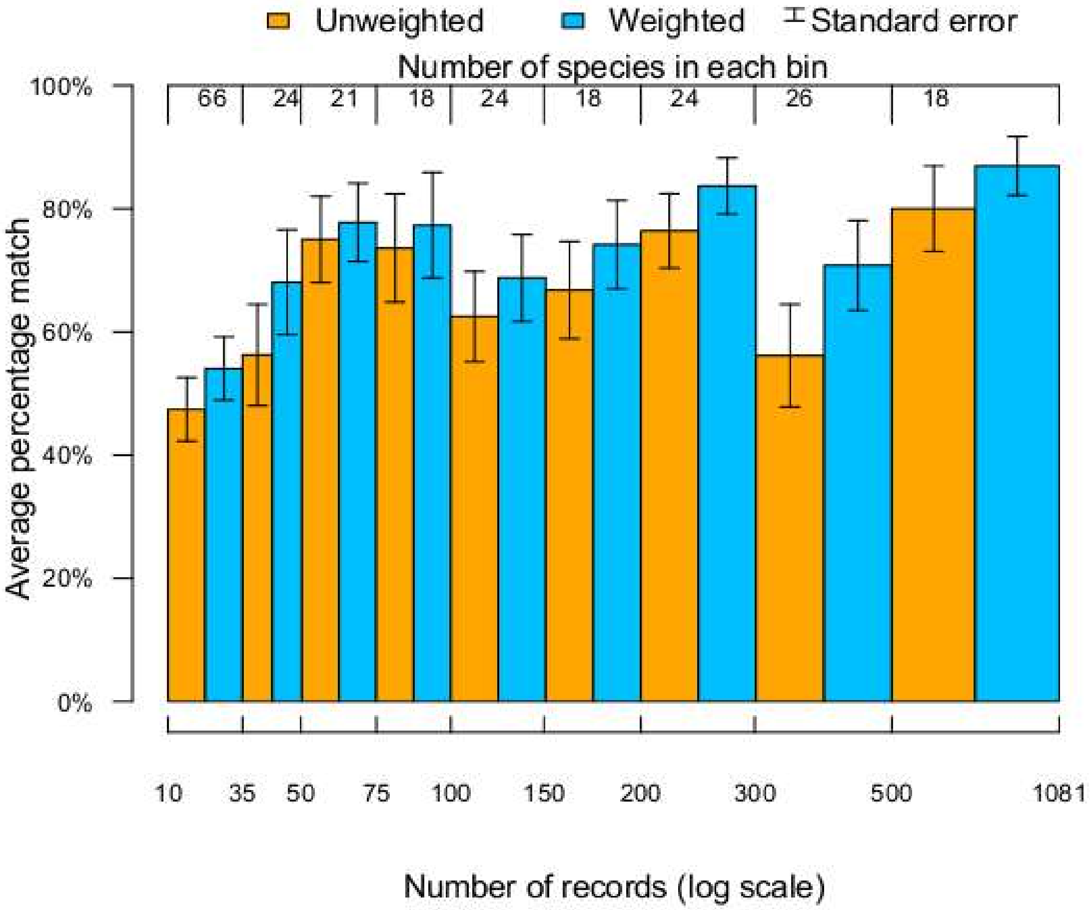

Fig. A C2.2.0-2 Comparison of original and weighted correlation index showing how they match the validation data. Species are in bins of the number of records (using the records without removal, as used in the weighted version). The unweighted version of the analysis that chose the most abundant habitat to represent each location matched the Luff validation data less well regardless of the number of records.

De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566–3574. doi:10.1890/08-1823.1

Appendix C2.3. Vector and matrix calculations of the Phi coefficient

The Phi coefficient can be calculated in two ways, either for each habitat of interest one at a time using three vectors, as shown in the main paper or by creating a matrix of the weighting of each habitat and calculating vector versions of N_p and n_p and subsequently a vector giving Phi values for all the habitats simultaneously. The vector version is easier to understand and is how one would calculate the Phi coefficient for a single habitat. The matrix example is computationally more efficient (in particular when running the permutation test) and elegantly gives the result for all habitats together. The vectors and matrix are different for each species and here we show an example for one species.

A C2.3.1. Vector version

If the vector version is used, one calculates the phi coefficient separately for each habitat of interest.

Table A C2.3.0-1 Example of the vectors that can be used in calculating the Phi coefficient for each individual habitat, showing the, proportion of each habitat within each location and the binary presence data, in this case for the species Abax parallelepipedus (see Appendix 2 for matrix version of this information and equations). (Identical to table 1 in the main text)

Location ID	**LCM2015 habitat**	**Heather habitat vector (h)**	**Weight vector (w)**	**Species vector (s)**
1	Heather grassland	0	1.00	0
2	Supralittoral sediment	0	1.00	0
3	Heather grassland	0	1.00	0
4	Acid grassland	0	0.02	1
4	Inland rock	0	0.59	1
4	Heather	1	0.39	1
5	Inland rock	0	1.00	0
6	Heather	1	0.76	0
6	Improved grassland	0	0.24	0
7	Inland rock	0	1.00	1
…	…	⋮	⋮	⋮

All three vectors have length L

<u>Unweighted</u>

$N =$ L or “the length of the habitat vector”

$N_p = \sum_{i=1}^{\mathrm{L}} h_i$ or “the sum of all values in the habitat vector”

$n = \sum_{i=1}^{L} s_i$ or “the sum of the species vector”

$n_p = \boldsymbol{h} \cdot \boldsymbol{s} = \sum_{i=1}^{\mathrm{L}} h_i s_i$ or “the sum of the product of the habitat and species vectors”

<u>Weighted</u>

$N = \sum_{i=1}^{L} w_i$ or “the sum of all values in the weighting vector”

$n = \boldsymbol{w} \cdot \boldsymbol{s} = \sum_{i=1}^{\mathrm{L}} w_i s_i$ or “sum of the product of the weighting vector and species vector”

$N_p^w = \boldsymbol{w} \cdot \boldsymbol{h}$ or $N_p^w = \sum_{i=1}^{\mathrm{L}} w_i h_i$ or “sum of the product of the weighting vector and the habitat of interest vector”

$n_p^w = \sum_{i=1}^{\mathrm{L}} w_i h_i s_i$ or “the sum of the product of all three vectors, the weighting, the habitat of interest and the species presence”

$$\Phi^w = \frac{N \times n_p^w - n \times N_p^w}{\sqrt{(N \times n - n^2) \times \left(N \times N_p^w - (N_p^w)^2\right)}}$$

An example of the output:

$$\Phi^w = 0.56$$

A C2.3.2. Matrix version

Creating a habitat matrix allows one to obtain the phi coefficient simultaneously for all habitats, returning a vector of phi values.

Table A C2.3.1 Showing how weighting for multiple habitats can be represented as a matrix, giving context to the matrix which is then shown below.

Location ID	**Acid grassland**	**Heather**	**Heather grassland**	**Improved grassland**	**Inland rock**	**Supralittoral sediment**	**…**	K
1	0.00	0.00	1.00	0.00	0.00	0.00	…	0.00
2	0.00	0.00	0.00	0.00	0.00	1.00	…	0.00
3	0.00	0.00	1.00	0.00	0.00	0.00	…	0.00
4	0.02	0.39	0.00	0.00	0.59	0.00	…	0.00
5	0.00	0.00	0.00	0.00	1.00	0.00	…	0.00
6	0.00	0.76	0.00	0.24	0.00	0.00	…	0.00
7	0.00	0.00	0.00	0.00	1.00	0.00	…	0.00
…	…	…	…	…	…		…	0.00…
N	0	0	0	0	0	0	…	0.00

Let **H** be the habitat matrix of length N and width K, where $N = No.sites$ and $K = No.habitats$.

$$\boldsymbol{H} = \begin{bmatrix} 0.00 & 0.00 & 1.00 & 0.00 & 0.00 & 0.00 & \cdots & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 1.00 & \cdots & 0.00 \\ 0.00 & 0.00 & 1.00 & 0.00 & 0.00 & 0.00 & \cdots & 0.00 \\ 0.02 & 0.39 & 0.00 & 0.00 & 0.59 & 0.00 & \cdots & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 1.00 & 0.00 & \cdots & 0.00 \\ 0.00 & 0.76 & 0.00 & 0.24 & 0.00 & 0.00 & \cdots & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 1.00 & 0.00 & \cdots & 0.00 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & \cdots & 0.00 \end{bmatrix}$$

Let **s** be the species vector of length N.

$$\boldsymbol{s} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 1 \\ 0 \\ 0 \\ 1 \\ \vdots \\ 0 \end{bmatrix}$$

Both weighted and unweighted

$$n = \sum_{i=1}^{\mathrm{N}} s_i$$

$$\boldsymbol{N_p} = \sum_{i=1}^{N} H_{ij}$$

$$\boldsymbol{n_p} = \sum_{i=1}^{N} s_i \times H_{ij}$$

$$\boldsymbol{\varphi^w} = \frac{N \times \boldsymbol{n_p^w} - n \times \boldsymbol{N_p^w}}{\sqrt{(N \times n - n^2) \times \left(N \times \boldsymbol{N_p^w} - \boldsymbol{N_p^w}^2\right)}}$$

An example of the output:

$$\boldsymbol{\varphi^w} = [0.20 \quad -0.15 \quad 0.05 \quad -0.25 \quad 0.01 \quad 0.03 \quad \ldots \quad -0.08]$$

Appendix C2.4. Scripts for calculating correlation index

The R package published as PhiCor (https://github.com/Zabados/PhiCor). CorrelationIndex.R is the version that was used for analysis, before being turned into package.

See scripts at www.ecography.org/appendix/ecog-04295:

- CorrelationIndex.R
- CompileJasminOutputs.r
- JasminRScript.r
- JasminSubmitRBatch.job
- Preprocess.r
- Validation.r

Appendix C2.5. Outputs

https://doi.org/10.5285/ce0a6690-9277-4880-a20a-b30477bf8646

The output data can be explored at https://shiny-apps.ceh.ac.uk/CarabidData/

Appendix C2.6. Specialist *vs* generalist analysis

A C2.6.1. Methods

Some of the species analysed using the weighted correlation index appear to have very few positively correlated habitats. We tested if this was related to whether the species is classified as a specialist (stenotopic) or generalist (eurytopic) species. Using information from several sources (H Turin & Denboer, 1988; Desender & Turin, 1989; Hans Turin, 2000; Fowles, 2004; Bates, Sadler, Fowles, & Butcher, 2005; Bates, Sadler, & Fowles, 2007; Pozsgai, Baird, Littlewood, Pakeman, & Young, 2016) we assigned each species a score from one (stenotopic) to five (eurytopic) and compared this to the number of positively correlated habitats.

A C2.6.2. Results

The boxplot in Figure A C2.6.1 suggests specialist species have fewer positively associated habitats, i.e. they specialise on fewer habitats. There is a lot of variation in the number of positive habitats for each specialist generalist score. Figure A C2.6.1 shows there is also a positive relationship between the score and the number of presence records, with those classed as generalist having more records, although there is a lot of variation.

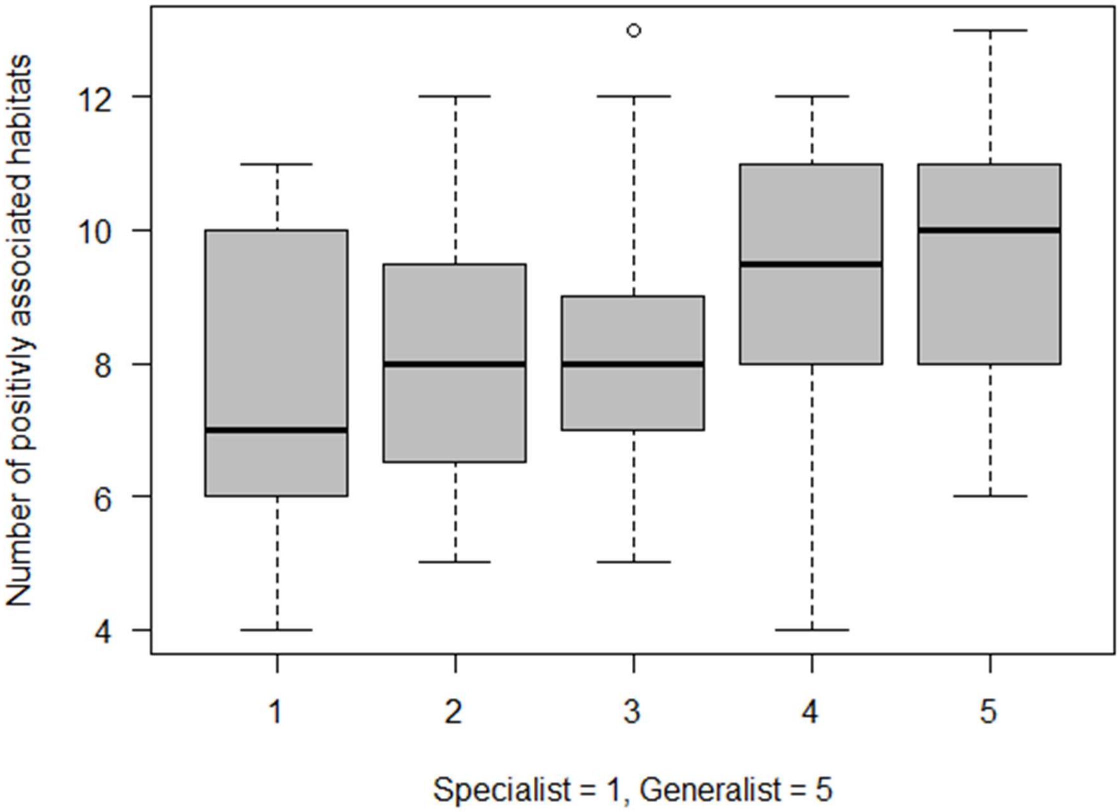

Figure A C2.6.1 Boxplot showing the relation between specialist to generalist and then number of positively correlated habitats derived using the weighted correlation index.

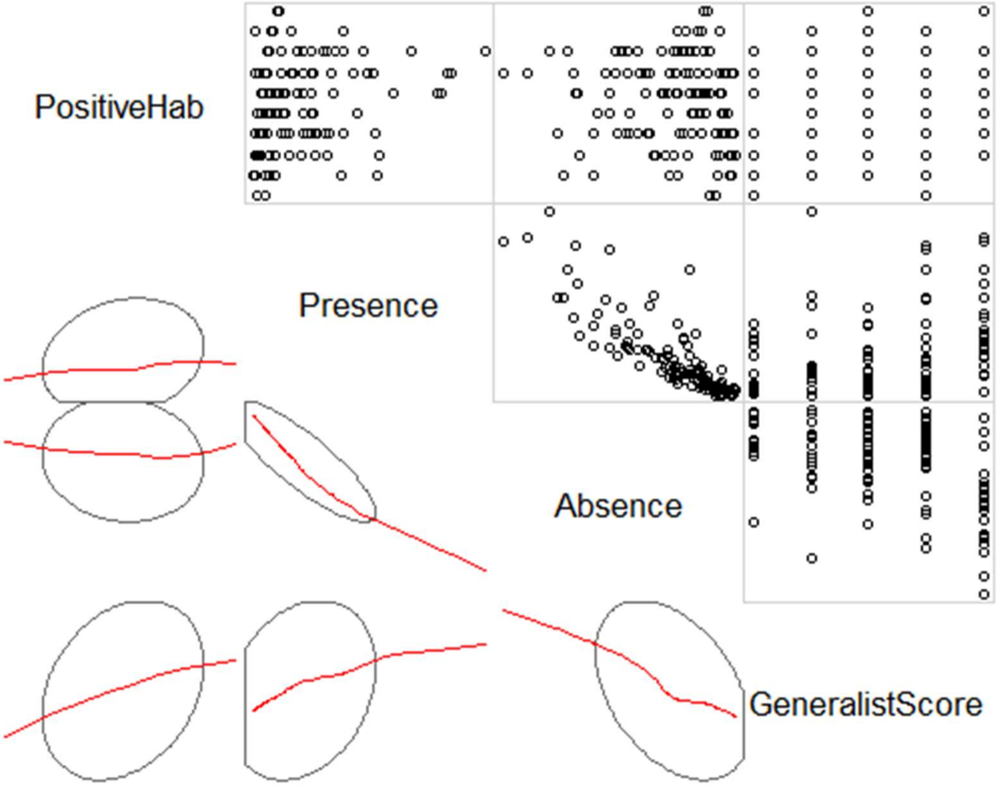

Figure A C2.6.2 Correlogram showing correlation between scored specialist vs generalist, number of presence and absence records and the number of positive habitats for each species. Confidence ellipse and smoothed line in lower left of graph.

Bates, A. J., Sadler, J. P., & Fowles, A. P. (2007). Livestock trampling reduces the conservation value of beetle communities on high quality exposed riverine sediments. *Biodiversity and Conservation*, *16*(5), 1491–1509. doi:10.1007/s10531-006-9028-7

Bates, A. J., Sadler, J. P., Fowles, A. P., & Butcher, C. R. (2005). Spatial dynamics of beetles living on exposed riverine sediments in the upper River Severn: method development and preliminary results. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*(2), 159–174. doi:10.1002/aqc.642

Desender, K., & Turin, H. (1989). Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four West European countries since 1950 (Coleoptera: Carabidae, cicindelidae). *Biological Conservation*, *48*(4), 277–294. doi:10.1016/0006-3207(89)90103-1

Fowles, A. (2004). Specialist Coleoptera of Exposed Riverine Sediments (ERS). Retrieved 9 April 2018, from https://yrefail.net/Coleoptera/ersqi.htm

Pozsgai, G., Baird, J., Littlewood, N. A., Pakeman, R. J., & Young, M. (2016). Interspecific networks in ground beetle (Coleoptera: Carabidae) assemblages. *Ecological Indicators*, *68*(SI), 134–141. doi:10.1016/j.ecolind.2015.11.031

Turin, H. (2000). *De Nederlandse loopkevers : verspreiding en oecologie (Coleoptera: Carabidae)*. Leiden; Utrecht; Leiden: Nationaal Natuurhistorisch Museum ; KNNV

Uitgeverij ; European Invertebrate Survey, Nederland.

Turin, H., & Denboer, P. J. (1988). Changes in the Distribution of Carabid Beetles in The Netherlands Since 1880 .2. Isolation of Habitats and Long-term Time Trends in the Occurrence of Carabid Species with Different Powers of Dispersal (Coleoptera, Carabidae). *Biological Conservation*, *44*(3), 179–200. doi:10.1016/0006-3207(88)90101-2

Appendix C2.7. Group equalised analysis

A C2.7.1. Methods

The group equalised version of the correlation index (equation A C2.7.1) (Tichy & Chytry, 2006; De Cáceres & Legendre, 2009) is similar to the non group-equalised version and contains the species presence absence vector. It differs by containing all of the habitat of interest vectors, for all habitats, which are all needed to calculate the number of habitats, averages of species' occurrences, and the number of locations within each habitat, to equalise the size of the groups.

$$\varphi^{g} = \frac{N \times \mathrm{n}_p^{g} - \mathrm{n}^{g} \times \mathrm{N}_p^{g}}{\sqrt{\left(\times\, \mathrm{n}^{g} - \mathrm{n}^{g^2}\right) \times \left(N \times \mathrm{N}_p^{g} - \mathrm{N}_p^{g^2}\right)}} \qquad \textit{eqn A C2.7.2}$$

Where N is the total number of locations (the length of the habitat vector), N_p^g is the average number of locations per habitat (N divided by number of habitats), n^g is the average number of occurrences in a habitat (the sum of the proportion of locations with occurrence for each habitat, divided by total number of habitats and multiplied by the number of locations), and n_p^g is the number of occurrences in habitat of interest inflated by the proportion of total number of locations over the total number of locations if all habitats had the same number of locations as the habitat of interest.

We created a weighted version of the index (equation A C2.7.2).

$$\varphi^{gw} = \frac{N \times \mathrm{n}_p^{gw} - \mathrm{n}^{gw} \times \mathrm{N}_p^{g}}{\sqrt{\left(\times\, \mathrm{n}^{gw} - \mathrm{n}^{gw2}\right) \times \left(N \times \mathrm{N}_p^{g} - \mathrm{N}_p^{g^2}\right)}} \qquad \textit{eqn A C2.7.3}$$

In the same way as the weighted non-group equalised version presented in the main body of the paper, this version added a third non-binary vector of the weighting of each habitat at each location which weights the other values. N is still the total number of locations, but now calculable as the sum of the weighting vector and N_p^g is still the average number of locations per habitat (N divided by number of habitats). n^{gw} is now a version of n^{g} in which the number of occurrences within each habitat and the number of locations is weighted $\mathrm{n}^{gw} = N_p^g \times \sum_{k=1}^{K} n_k^w / N_k^w$. K is total number of habitats, n_k^w is the weighted occurrence, and N_k^w the weighted amount of habitat in habitat k. n_p^{gw} is the number of occurrences in habitat of interest (n_p) inflated by the proportion of total number of locations over the total number of locations if all habitats had the same number of locations and weighting as the habitat of interest ($\mathrm{n}_p \times N/(K \cdot N_p^w)$; N_p^w is N_k^w for the habitat of interest).

A C2.7.2. Results

The unweighted group equalised analysis identified on average 64.5% (using 187 species) of Luff habitats and the weighted group equalised analysis 67.7% (using 239 species). The full results are included in the outputs as Rg and with p-values as pRg.

Looking at the weighted version only, the results suggest, as would be expected that the more common habitats are the most preferred in the non-group equalised analysis simply because they are common. For example, *Abax parallelepipedus* has broadleaf woodland as the most preferred in the non group equalised version, followed by coniferous and then acid grassland and heathland habitats. Broadleaf woodland has the largest amount of habitat followed by improved grassland, both one or two orders of magnitude larger than the other habitats (Figure A C2.7.1). The patterns of phi values are similar relative to the amount of habitat, but those with the most and least are adjusted either towards or away from zero respectively. In the group equalised version, broadleaf woodland moves down the preference to fifth, similarly improved grassland moves from 19th to 14th, becoming less negatively associated.

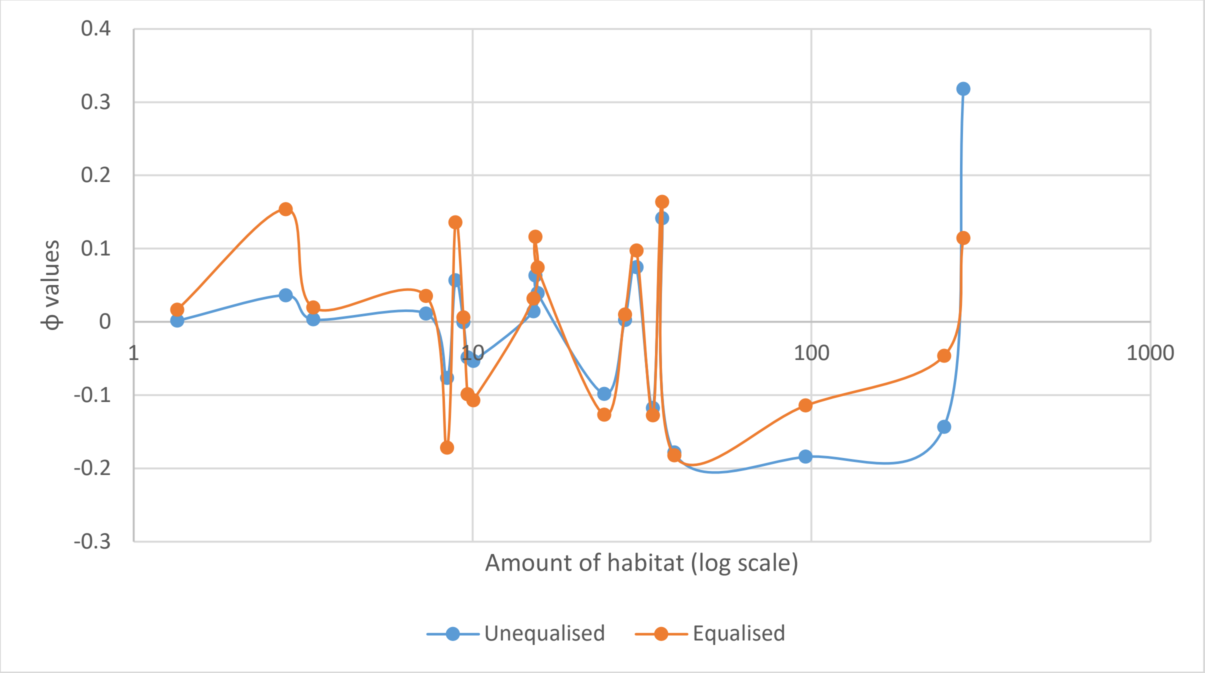

Figure A C2.7.1 Showing the general lack of correlation between the amount of habitat and the calculated φ value, but that the equalised version adjusts the habitats with the least and most habitat.

De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566–3574. doi:10.1890/08-1823.1

Tichy, L., & Chytry, M. (2006). Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, *17*(6), 809–818. doi:10.1111/j.1654-1103.2006.tb02504.x

Appendix C2.8. NBN citation 7

See file NBN_full_citation.csv in the appendices of the published paper.

Appendix for Chapter 4

Using a logged version of the number of patches when fitting alpha-, beta- and gamma-diversity increase the fit in all cases (likelihood ratio test ChiSq 5475.8 (p <0.01), 2578.8 (p <0.01) and 77.8 (p <0.01) respectively). In the case of alpha-diversity, it caused the AIC to jump from 80.7 to 5556.5, for gamma-diversity the AIC increased from 9936.0 to 9858.2 in both cases it was therefore inappropriate to log the number of patches. For beta-diversity, logging the number of patches changed the AIC from -3913.2 to -6492.0 and therefore logging the number of patches was appropriate for the beta-regression method we used for beta-diversity.

Table A C4.1| Comparison of Gamma-diversity relationship between 10% and 40% cover of habitat showing no significant difference.

	Baseline		Habitat dependency		Specialism	
Intercept 10%	**3.45**	**(CI [3.43e+00, 3.47e+00], SE 8.68e-03)**	**2.93**	**(CI [2.91e+00, 2.95e+00], SE 1.12e-02)**	**3.21**	**(CI [3.19e+00, 3.23e+00], SE 9.66e-03)**
Add intercept 40%	-3.45E-03	(CI [-2.73e-02, 2.04e-02], SE 1.22e-02)	2.04E-03	(CI [-2.86e-02, 3.27e-02], SE 1.56e-02)	6.93E-03	(CI [-1.96e-02, 3.34e-02], SE 1.35e-02)
Slope 10%	3.49E-06	(CI [-3.91e-06, 1.09e-05], SE 3.77e-06)	2.17E-05	**(CI [1.22e-05, 3.11e-05], SE 4.82e-06)**	2.65E-05	**(CI [1.84e-05, 3.46e-05], SE 4.14e-06)**
Add slope 40%	3.74E-06	(CI [-5.78e-06, 1.33e-05], SE 4.86e-06)	-4.16E-06	(CI [-1.62e-05, 7.85e-06], SE 6.13e-06)	-5.77E-06	(CI [-1.61e-05, 4.55e-06], SE 5.26e-06)

Table A C4.2| ***Comparison of the alpha-diversity relationship between 10% and 40% cover of habitat showing significant differences.***

	Baseline		Habitat dependency		Specialism	
Intercept 10%	**2.03**	**(CI [1.96e+00, 2.11e+00], SE 3.83e-02)**	**1.31**	**(CI [1.25e+00, 1.38e+00], SE 3.52e-02)**	**1.6**	**(CI [1.53e+00, 1.67e+00], SE 3.61e-02)**
Add intercept 40%	-0.0455	(CI [-1.51e-01, 5.98e-02], SE 5.37e-02)	-0.0351	(CI [-1.32e-01, 6.16e-02], SE 4.93e-02)	-0.0513	(CI [-1.50e-01, 4.77e-02], SE 5.05e-02)
Linear 10%	**-0.00222**	**(CI [-2.33e-03, -2.11e-03], SE 5.73e-05)**	**-0.00199**	**(CI [-2.10e-03, -1.89e-03], SE 5.34e-05)**	**-0.00206**	**(CI [-2.16e-03, -1.95e-03], SE 5.48e-05)**
Add linear 40%t	**0.000356**	**(CI [2.15e-04, 4.98e-04], SE 7.24e-05)**	**0.000285**	**(CI [1.53e-04, 4.17e-04], SE 6.73e-05)**	**0.000345**	**(CI [2.10e-04, 4.81e-04], SE 6.92e-05)**
Squared 10%	**0.000000244**	**(CI [2.25e-07, 2.63e-07], SE 0.00e+00)**	**0.000000215**	**(CI [1.98e-07, 2.33e-07], SE 0.00e+00)**	**0.000000224**	**(CI [2.05e-07, 2.42e-07], SE 0.00e+00)**
Add squared 40%	**-8.38E-08**	**(CI [-1.06e-07, -6.17e-08], SE 0.00e+00)**	**-6.73E-08**	**(CI [-8.79e-08, -4.67e-08], SE 0.00e+00)**	**-7.82E-08**	**(CI [-9.93e-08, -5.70e-08], SE 0.00e+00)**

Table A C4.3| ***Comparison of the beta-diversity relationship between 10% and 40% cover of habitat showing no significant difference.***

	Baseline		Habitat dependency		Specialism	
Intercept 10%	**-1.42**	**(CI [-1.49e+00, -1.35e+00], SE 3.73e-02)**	**-1.04**	Intercept 10%	**-1.42**	**(CI [-1.49e+00, -1.35e+00], SE 3.73e-02)**
Add intercept 40%	0.00256	(CI [-9.94e-02, 1.04e-01], SE 5.20e-02)	-0.063	Add intercept 40%	0.00256	(CI [-9.94e-02, 1.04e-01], SE 5.20e-02)
Slope 10%	**0.679**	**(CI [6.61e-01, 6.98e-01], SE 9.37e-03)**	**0.341**	Slope 10%	**0.679**	**(CI [6.61e-01, 6.98e-01], SE 9.37e-03)**
Add slope 40%	-0.00438	(CI [-2.94e-02, 2.06e-02], SE 1.28e-02)	0.00573	Add slope 40%	-0.00438	(CI [-2.94e-02, 2.06e-02], SE 1.28e-02)
(phi)	**46**	**(CI [4.22e+01, 4.99e+01], SE 1.94e+00)**	**20.8**	(phi)	**46**	**(CI [4.22e+01, 4.99e+01], SE 1.94e+00)**

Table A C4.4| ***Overall number of patches to gamma-diversity regression results comparing linear, squared, and cubed fits of a generalized linear model with a Poisson distribution. A linear relationship best fits the relationship between the number of patches and gamma-diversity.***

Treatment	Fitted	Habitat cover	Intercept		number of patches		number of patches^2		number of patches^3		N	AIC
Baseline	Linear	10%	3.45	(SE 8.68e-03, p <0.01)	3.49E-06	(SE 3.77E-06, p 0.36)					587	3310
Baseline	Square	10%	3.45	(SE 9.60e-03, p <0.01)	3.98E-06	(SE 1.43E-05, p 0.78)	0.00E+00	(SE 0.00E+00, p 0.97)			587	3310
Baseline	Cube	10%	3.44	(SE 1.05e-02, p <0.01)	4.52E-05	(SE 3.17E-05, p 0.15)	-2.07E-08	(SE 0.00E+00, p 0.15)	0.00E+00	(SE 0.00e+00, p 0.15)	587	3310
Baseline	Linear	40%	3.45	(SE 8.52e-03, p <0.01)	7.23E-06	(SE 3.06E-06, p 0.02)					584	3290
Baseline	Square	40%	3.45	(SE 9.45e-03, p <0.01)	1.31E-05	(SE 1.10E-05, p 0.23)	0.00E+00	(SE 0.00E+00, p 0.58)			584	3290
Baseline	Cube	40%	3.44	(SE 1.04e-02, p <0.01)	3.25E-05	(SE 2.84E-05, p 0.25)	0.00E+00	(SE 0.00E+00, p 0.42)	0.00E+00	(SE 0.00e+00, p 0.46)	584	3290
Habitat dependency	Linear	10%	2.93	(SE 1.12e-02, p <0.01)	2.17E-05	(SE 4.82E-06, p <0.01)					586	3250
Habitat dependency	Square	10%	2.91	(SE 1.25e-02, p <0.01)	1.04E-04	(SE 1.80E-05, p <0.01)	0.00E+00	(SE 0.00E+00, p <0.01)			586	3230
Habitat dependency	Cube	10%	2.89	(SE 1.36e-02, p <0.01)	1.88E-04	(SE 3.95E-05, p <0.01)	-5.69E-08	(SE 1.81E-08, p <0.01)	0.00E+00	(SE 0.00e+00, p 0.02)	586	3230
Habitat dependency	Linear	40%	2.93	(SE 1.09e-02, p <0.01)	1.75E-05	(SE 3.78E-06, p <0.01)					589	3300
Habitat dependency	Square	40%	2.92	(SE 1.22e-02, p <0.01)	6.49E-05	(SE 1.38E-05, p <0.01)	0.00E+00	(SE 0.00E+00, p <0.01)			589	3290
Habitat dependency	Cube	40%	2.9	(SE 1.35e-02, p <0.01)	1.26E-04	(SE 3.60E-05, p <0.01)	-3.15E-08	(SE 0.00E+00, p 0.02)	0.00E+00	(SE 0.00e+00, p 0.07)	589	3280
Specialism	Linear	10%	3.21	(SE 9.66e-03, p <0.01)	2.65E-05	(SE 4.14E-06, p <0.01)					591	3370
Specialism	Square	10%	3.19	(SE 1.08e-02, p <0.01)	8.21E-05	(SE 1.56E-05, p <0.01)	0.00E+00	(SE 0.00E+00, p <0.01)			591	3360
Specialism	Cube	10%	3.18	(SE 1.18e-02, p <0.01)	1.56E-04	(SE 3.44E-05, p <0.01)	-4.67E-08	(SE 1.57E-08, p <0.01)	0.00E+00	(SE 0.00e+00, p 0.02)	591	3350
Specialism	Linear	40%	3.22	(SE 9.45e-03, p <0.01)	2.07E-05	(SE 3.25E-06, p <0.01)					592	3370
Specialism	Square	40%	3.2	(SE 1.05e-02, p <0.01)	7.24E-05	(SE 1.19E-05, p <0.01)	0.00E+00	(SE 0.00E+00, p <0.01)			592	3360
Specialism	Cube	40%	3.18	(SE 1.17e-02, p <0.01)	1.83E-04	(SE 3.12E-05, p <0.01)	-5.25E-08	(SE 0.00E+00, p <0.01)	0.00E+00	(SE 0.00e+00, p 1.46e-04)	592	3340

Table A C4.5| ***Overall number of patches to alpha-diversity regression results comparing linear, squared, and cubed fits of a generalized linear model with a gamma distribution. A cubed relationship best fits the relationship between the number of patches and alpha-diversity.***

Treatment	Fitted	Habitat cover	Intercept		number of patches		number of patches^2		number of patches^3		N	AIC
Baseline	Linear	10%	1.85	(SE 4.41e-02)	-8.33E-04	(SE 1.93e-05)					587	2150
Baseline	Square	10%	2.03	(SE 3.78e-02)	-2.22E-03	(SE 5.65e-05)	2.44E-07	(SE 0.00e+00)			587	1720
Baseline	Cube	10%	2.2	(SE 3.09e-02)	-4.11E-03	(SE 9.45e-05)	1.18E-06	(SE 4.28e-08)	0.00E+00	(SE 0.00e+00)	587	1330
Baseline	Linear	40%	1.79	(SE 4.55e-02)	-6.27E-04	(SE 1.67e-05)					584	2270
Baseline	Square	40%	1.99	(SE 3.82e-02)	-1.86E-03	(SE 4.49e-05)	1.60E-07	(SE 0.00e+00)			584	1770
Baseline	Cube	40%	2.17	(SE 3.09e-02)	-3.79E-03	(SE 8.54e-05)	9.55E-07	(SE 3.33e-08)	0.00E+00	(SE 0.00e+00)	584	1350
Habitat dependency	Linear	10%	1.13	(SE 3.97e-02)	-7.75E-04	(SE 1.80e-05)					586	1400
Habitat dependency	Square	10%	1.31	(SE 3.46e-02)	-1.99E-03	(SE 5.26e-05)	2.15E-07	(SE 0.00e+00)			586	999
Habitat dependency	Cube	10%	1.48	(SE 2.76e-02)	-3.66E-03	(SE 8.45e-05)	1.05E-06	(SE 3.89e-08)	0.00E+00	(SE 0.00e+00)	586	637
Habitat dependency	Linear	40%	1.07	(SE 4.25e-02)	-5.59E-04	(SE 1.54e-05)					589	1530
Habitat dependency	Square	40%	1.28	(SE 3.51e-02)	-1.71E-03	(SE 4.16e-05)	1.48E-07	(SE 0.00e+00)			589	1020
Habitat dependency	Cube	40%	1.45	(SE 2.90e-02)	-3.32E-03	(SE 8.06e-05)	8.12E-07	(SE 3.14e-08)	0.00E+00	(SE 0.00e+00)	589	660
Specialism	Linear	10%	1.42	(SE 4.14e-02)	-7.86E-04	(SE 1.87e-05)					591	1750
Specialism	Square	10%	1.6	(SE 3.50e-02)	-2.06E-03	(SE 5.32e-05)	2.24E-07	(SE 0.00e+00)			591	1330
Specialism	Cube	10%	1.76	(SE 2.96e-02)	-3.68E-03	(SE 9.05e-05)	1.04E-06	(SE 4.15e-08)	0.00E+00	(SE 0.00e+00)	591	1000
Specialism	Linear	40%	1.36	(SE 4.33e-02)	-5.86E-04	(SE 1.58e-05)					592	1840
Specialism	Square	40%	1.55	(SE 3.63e-02)	-1.71E-03	(SE 4.34e-05)	1.45E-07	(SE 0.00e+00)			592	1370
Specialism	Cube	40%	1.73	(SE 2.98e-02)	-3.49E-03	(SE 8.38e-05)	8.76E-07	(SE 3.26e-08)	0.00E+00	(SE 0.00e+00)	592	976

Table A C4.6| ***Overall log number of patches to beta-diversity regression results comparing linear, squared, and cubed fits of a maximum likelihood regression with a beta distribution. A linear relationship best fits the relationship between log number of patches and beta-diversity.***

Treatment	Fitted	Habitat cover	Intercept		number of patches		Phi		number of patches^2		number of patches^3		nobs	df. null	log Lik	AIC
Baseline	Linear	10%	-1.4	CI -1.48e+00, -1.32e+00, SE 4.01e-02	0.67	CI 6.51e-01, 6.91e-01, SE 1.02e-02	40.1	CI 3.54e+01, 4.48e+01, SE 2.39e+00					587	0.96	585.00	1170.32
Baseline	Square	10%	-1.15	CI -1.29e+00, -9.96e-01, SE 7.60e-02	0.52	CI 4.47e-01, 6.00e-01, SE 3.92e-02	43.3	CI 3.81e+01, 4.85e+01, SE 2.65e+00	0.0173	CI 8.69e-03, 2.59e-02, SE 4.38e-03			587	0.97	585.00	1177.14
Baseline	Cube	10%	-0.43	CI -7.32e-01, -1.24e-01, SE 1.55e-01	-0.12	CI -3.76e-01, 1.28e-01, SE 1.29e-01	44.4	CI 3.91e+01, 4.97e+01, SE 2.71e+00	0.178	CI 1.18e-01, 2.39e-01, SE 3.08e-02	-0.0115	CI -1.57e-02, -7.23e-03, SE 2.17e-03	587	0.96	585.00	1190.83
Baseline	Linear	40%	-1.44	CI -1.51e+00, -1.37e+00, SE 3.52e-02	0.68	CI 6.65e-01, 7.01e-01, SE 9.07e-03	54.1	CI 4.78e+01, 6.04e+01, SE 3.21e+00					584	0.97	582.00	1241.95
Baseline	Square	40%	-1.08	CI -1.20e+00, -9.53e-01, SE 6.41e-02	0.47	CI 4.05e-01, 5.36e-01, SE 3.34e-02	63.3	CI 5.57e+01, 7.09e+01, SE 3.86e+00	0.0253	CI 1.79e-02, 3.28e-02, SE 3.81e-03			584	0.98	582.00	1259.66
Baseline	Cube	40%	-0.23	CI -4.74e-01, 1.80e-02, SE 1.25e-01	-0.30	CI -5.01e-01, -9.45e-02, SE 1.04e-01	66.8	CI 5.89e+01, 7.48e+01, SE 4.05e+00	0.217	CI 1.68e-01, 2.66e-01, SE 2.48e-02	-0.0137	CI -1.71e-02, -1.03e-02, SE 1.75e-03	584	0.97	582.00	1288.82
Habitat dependency	Linear	10%	-1.04	CI -1.13e+00, -9.50e-01, SE 4.58e-02	0.34	CI 3.23e-01, 3.58e-01, SE 8.92e-03	20.6	CI 1.83e+01, 2.29e+01, SE 1.18e+00					586	0.88	584.00	959.70
Habitat dependency	Square	10%	-1.12	CI -1.31e+00, -9.40e-01, SE 9.38e-02	0.38	CI 3.00e-01, 4.67e-01, SE 4.28e-02	20.6	CI 1.83e+01, 2.29e+01, SE 1.18e+00	-0.00439	CI -1.27e-02, 3.93e-03, SE 4.24e-03			586	0.93	584.00	1017.21
Habitat dependency	Cube	10%	-0.47	CI -8.43e-01, -1.05e-01, SE 1.88e-01	-0.16	CI -4.45e-01, 1.21e-01, SE 1.45e-01	21.1	CI 1.87e+01, 2.35e+01, SE 1.21e+00	0.121	CI 5.83e-02, 1.84e-01, SE 3.22e-02	-0.00844	CI -1.26e-02, -4.24e-03, SE 2.14e-03	586	0.92	584.00	1030.72
Habitat dependency	Linear	40%	-1.1	CI -1.19e+00, -1.02e+00, SE 4.53e-02	0.35	CI 3.30e-01, 3.64e-01, SE 8.71e-03	21	CI 1.87e+01, 2.34e+01, SE 1.21e+00					589	0.90	587.00	991.20
Habitat dependency	Square	40%	-1.57	CI -1.75e+00, -1.40e+00, SE 9.06e-02	0.58	CI 5.04e-01, 6.61e-01, SE 4.03e-02	22.1	CI 1.96e+01, 2.45e+01, SE 1.27e+00	-0.0235	CI -3.11e-02, -1.59e-02, SE 3.89e-03			589	0.93	587.00	1029.34
Habitat dependency	Cube	40%	-1.21	CI -1.57e+00, -8.60e-01, SE 1.80e-01	0.29	CI 2.55e-02, 5.51e-01, SE 1.34e-01	22.3	CI 1.98e+01, 2.48e+01, SE 1.28e+00	0.0425	CI -1.44e-02, 9.93e-02, SE 2.90e-02	-0.00431	CI -7.99e-03, -6.37e-04, SE 1.88e-03	589	0.92	587.00	1045.33
Specialism	Linear	10%	-1.21	CI -1.28e+00, -1.14e+00, SE 3.60e-02	0.43	CI 4.17e-01, 4.46e-01, SE 7.45e-03	37.4	CI 3.32e+01, 4.17e+01, SE 2.16e+00					591	0.93	589.00	1148.06
Specialism	Square	10%	-1.54	CI -1.68e+00, -1.40e+00, SE 7.25e-02	0.61	CI 5.42e-01, 6.74e-01, SE 3.38e-02	38.6	CI 3.43e+01, 4.30e+01, SE 2.23e+00	-0.0185	CI -2.52e-02, -1.18e-02, SE 3.41e-03			591	0.96	589.00	1192.19
Specialism	Cube	10%	-1.05	CI -1.33e+00, -7.63e-01, SE 1.46e-01	0.19	CI -3.19e-02, 4.11e-01, SE 1.13e-01	39.6	CI 3.51e+01, 4.40e+01, SE 2.29e+00	0.0793	CI 2.93e-02, 1.29e-01, SE 2.55e-02	-0.00664	CI -1.00e-02, -3.27e-03, SE 1.72e-03	591	0.95	589.00	1201.95
Specialism	Linear	40%	-1.2	CI -1.27e+00, -1.14e+00, SE 3.51e-02	0.43	CI 4.16e-01, 4.45e-01, SE 7.25e-03	38.8	CI 3.44e+01, 4.32e+01, SE 2.24e+00					592	0.93	590.00	1134.30
Specialism	Square	40%	-1.66	CI -1.80e+00, -1.53e+00, SE 6.86e-02	0.67	CI 6.09e-01, 7.32e-01, SE 3.15e-02	41.7	CI 3.70e+01, 4.64e+01, SE 2.41e+00	-0.0249	CI -3.10e-02, -1.87e-02, SE 3.13e-03			592	0.96	590.00	1182.24
Specialism	Cube	40%	-1.21	CI -1.48e+00, -9.49e-01, SE 1.36e-01	0.30	CI 9.38e-02, 4.98e-01, SE 1.03e-01	42.7	CI 3.78e+01, 4.75e+01, SE 2.47e+00	0.0609	CI 1.63e-02, 1.06e-01, SE 2.28e-02	-0.0057	CI -8.63e-03, -2.77e-03, SE 1.50e-03	592	0.95	590.00	1205.18

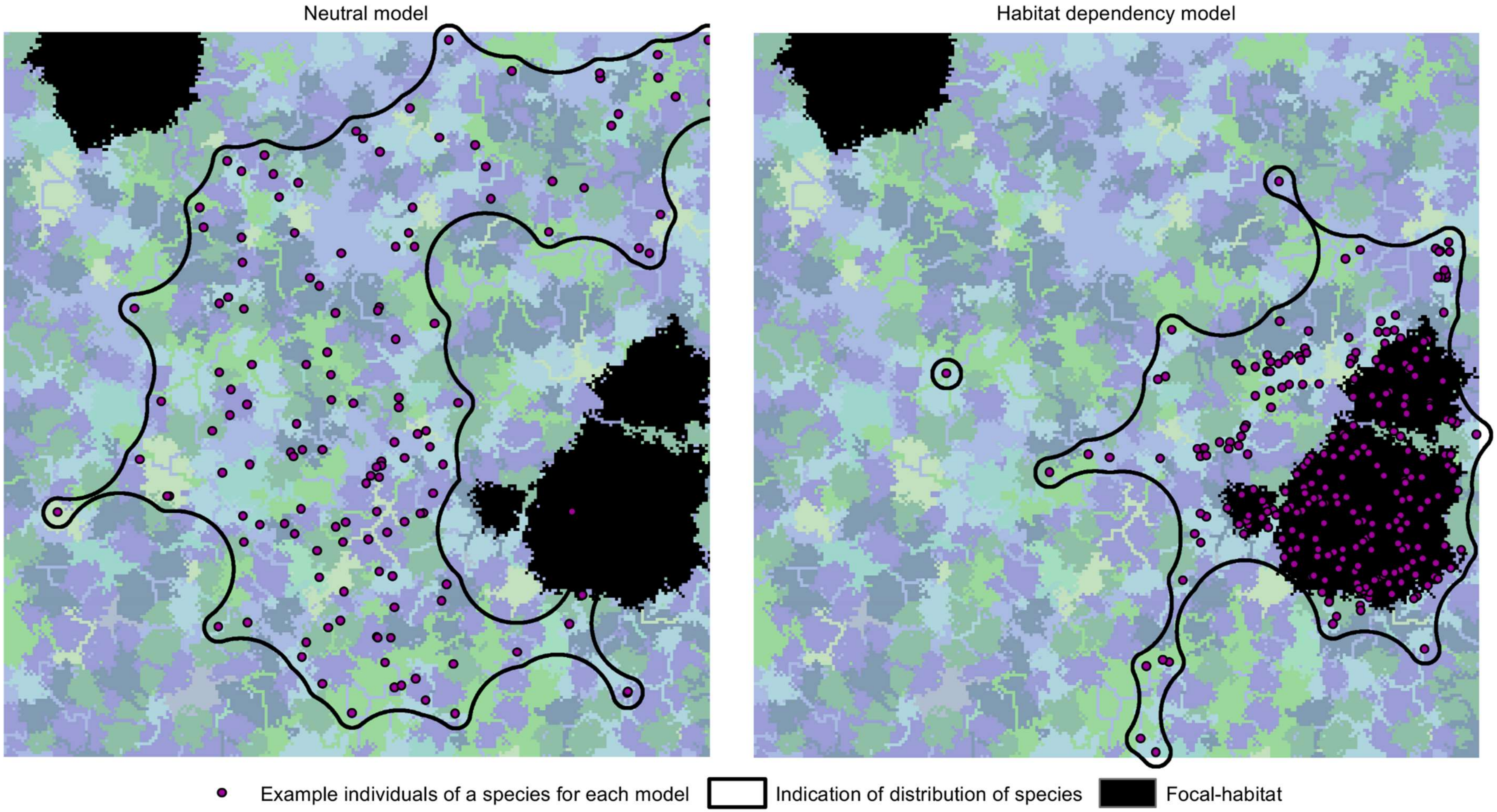

Figure A C4.1 ***Two example maps showing the distribution of individuals of a species in the baseline model and habitat dependency model run for illustrative purposes on the same land cover with four patches of the focal-habitat.*** *This shows that the baseline model, where individuals do not consider the habitat and are scattered randomly, can have voids with no individuals of a species. In the habitat dependency model, the species are more restricted to a single habitat or group of habitats.*