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Population dynamics in highly fragmented landscapes

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"Theory without fact is phantasy;
but fact without theory is chaos.
Divorced, both are useless;
united, they are equally essential and fruitful."

Charles Otis Whitman, *American zoologist*

Abstract

Understanding the effects of habitat fragmentation to ecosystems is key to elaborate the best policies to avoid species extinctions. Therefore, it is important to study how the populations and ecosystems respond to changes in the habitat distribution on landscapes. Recent debates of the topic in the ecology community have defended different points of view and conclusions on experiments and observations. In this project, we use numerical methods to simulate reaction-diffusion equations in artificial landscapes generated with different structural distributions while keeping the total habitat amount (HA) constant. This guarantees we are observing phenomena caused by *fragmentation per se*. We model fragmented landscapes as composed of two regions: habitat and matrix, which differ by reactions (logistic growth and death, respectively) and diffusivities. We discuss the net effects of fragmentation into the steady total population in artificial landscapes. These effects are dependent on the quality of matrix and, hence, we analyse three different scenarios: soft, intermediate and hostile matrices. In soft matrices, highly fragmented landscapes can support greater total population of a single species compared to slightly fragmented landscapes - and the opposite is true for hostile matrices. Regarding conservation purposes, highly fragmented landscapes eventually led to the extinction of species for a sufficiently hostile matrix in low HA. Quantitatively, we employed three statistical models and concluded that models where the effects of fragmentation and HA are interdependent presented the best statistical descriptions of average population density on landscapes. Our synthetic data also supported that fragmentation effects are not negligible compared to habitat loss, and effects of fragmentation considering linear HA effect and effects of *fragmentation per se* are similar in direction across the HA gradient. In conclusion, we argue that the model we present can be used to generate synthetic data in order to help to elucidate patterns on the debates about the effects of *fragmentation per se* into the ecological value of landscapes.

Keywords: Landscape; Habitat Fragmentation; *Fragmentation per se*; Reaction-diffusion Equations; Ecological value; Statistical models.

Fields of knowledge: Landscape Ecology; Theoretical Ecology; Population Dynamics; Mathematical Modelling.

Resumo

Entender os efeitos da fragmentação de habitat aos ecossistemas é essencial para a elaboração de melhores políticas de conservação de espécie. Assim, faz-se importante estudar como as populações e ecossistemas respondem a esse tipo de mudança na distribuição de habitat em paisagens. Debates recentes em ecologia têm confrontado diferentes perspectivas e conclusões em experimentos e observações. Neste projeto, usamos métodos numéricos para simular equações de reação-difusão em paisagens artificiais geradas com diferentes padrões configurações da mesma quantidade de habitat (*habitat amount*, HA). Isso garante que observamos padrões causados por *fragmentação per se*. Modelamos paisagens fragmentadas compostas por duas regiões: habitat e matriz, nas quais as reações são crescimento logístico e morte, respectivamente, e consideramos difusividades diferentes. Analisamos o efeito líquido da fragmentação na população total no estado estacionário em paisagens artificiais. Esses efeitos dependem da qualidade da matriz, e portanto, analisamos três cenários: matrizes branda, intermediária e hostil. Em matrizes brandas, paisagens altamente fragmentadas podem conter uma população total de uma única espécie maior que as paisagens pouco fragmentadas - e o contrário para matrizes hostís. Para fins de conservação, paisagens altamente fragmentadas eventualmente levaram a extinção da espécie para matrizes suficientemente hostís e pequena HA. Ademais, empregamos três modelos estatísticos e concluímos que os modelos em que os efeitos de fragmentação e HA são interdependentes apresentaram a melhor descrição estatística da densidade populacional média nas paisagens. Nossos dados sintéticos também apoiam efeitos de fragmentação não desprezíveis quando comparados com a perda de habitat, e os efeitos da fragmentação considerando efeitos lineares da HA e efeitos da *fragmentação per se* mostraram concordância sentido. Em suma, mostramos que o modelo apresentado pode ser usado para gerar dados sintéticos que formam uma ferramenta para elucidar padrões no debate sobre os efeitos de *fragmentação per se* no valor ecológico de paisagens.

Palavras-chave: Paisagem; Fragmentação de habitat; *Fragmentação per se*; Equações de reação-difusão; Valor ecológico; Modelos estatísticos.

Áreas do conhecimento: Ecologia de paisagem; Ecologia teórica; Dinâmica poplacional; Modelagem matemática.

Contents

Chapter 1

Introduction

J.A. Wiens (1999) defines landscape as "the template on which spatial patterns influence ecological processes", and it is the central feature in spatial ecology [1]. These landscapes are usually heterogeneous regions where the quantity or quality of abiotic factors (soil, water, sunlight *etc*) and biotic factors (vegetation, preys, predators, and so on) vary from one point to the other. Understanding the influence of these spatial patterns over several biological scales has been an immense endeavor thus far, and in the last few decades, mathematical models have intensely helped the construction of an ecological theory seeking to explain the patterns observed in nature as well as to relate microscopic processes to population emergent phenomena [2, 3, 4].

For instance, the limitation of population growth in a stationary regime of a single species is an emergent effect of intraspecific competition for resources and space among individuals. Supposing an homogeneous habitat, then the total population should scale linearly with its total area, as seen for habitat abundant landscapes in the schematic Fig. 1.1(a) [5, 6]. Furthermore, the presence of a threshold of habitat amount (HA), i.e., a minimum fraction of habitat in landscape to sustain a viable population, has been extensively reported under the name of *extinction threshold* [5, 6, 7, 8]. Hence, the process of habitat loss has been pointed out by several authors as the leading cause of extinctions in recent centuries [9, 10, 11].

Although the extinction threshold is known to always be present in the habitat loss process, it is not a sharp transition and its observed values vary between habitat fractions of 20% and 30% across landscapes, depending also on species and, specially, when fragmentation of habitat leads to sparse distributions of the remaining habitat in landscape [5, 6, 8, 9, 12]. In order to understand the mechanistic origins of the extinction threshold, several authors, including Andrén (1994) [5], suggest studying the impact of habitat fragmentation and percolation to population dynamics and conservation, introducing a new axis of complexity to the ecological value of landscapes, as in the schematic Fig. 1.1(b) [8, 9, 12].
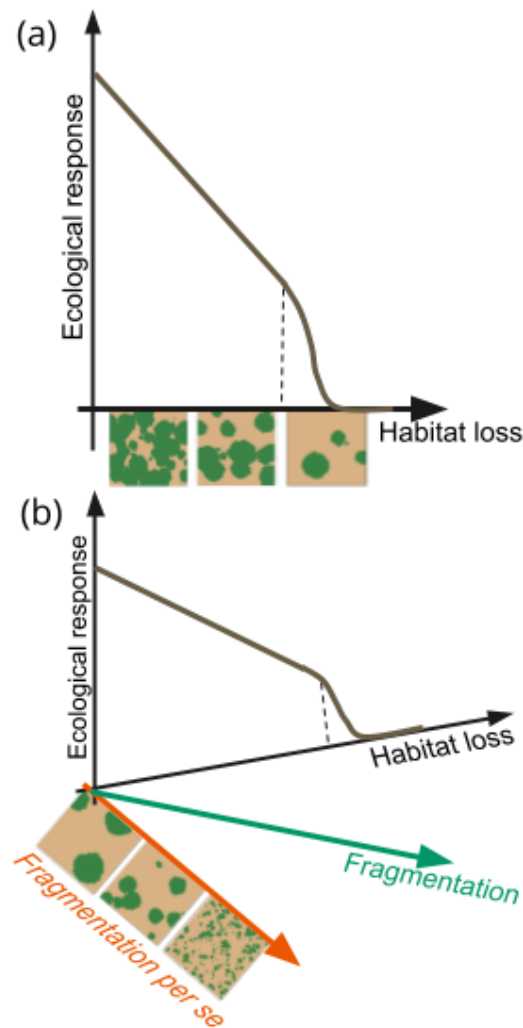
Figure 1.1: (a) Conceptualization of the negative effects of habitat loss, initially represented by a linear relationship between habitat amount and the ecological response of a landscape (i.e., population abundance or biodiversity) in habitat abundant landscapes, while for low habitat amounts we observe the presence of the extinction threshold as a function of habitat loss. (b) Ecologists propose adding a new dimension to the problem: habitat fragmentation. To refer exactly to different spatial distributions of the same habitat amount, the term *fragmentation per se* has been employed by several authors, and represented as a perpendicular axis to habitat loss.

In order to distinguish the process of fragmentation, which usually is related to habitat loss, from the different spatial configurations of the same HA, Fahrig (2003) [9] defines *fragmentation per se* as "the breaking apart of habitat, controlling for changes in habitat amount". In Fig. 1.1(b), we illustrate *fragmentation per se* as an axis perpendicular to habitat loss, representing its independence, while fragmentation is related to both habitat loss and its configuration. Some authors,

as Didham (2012) [10], criticize conceptualizing fragmentation controlling for HA, i.e. *fragmentation per se* , since it is generated in a fragmentation process which, necessarily, reduces HA. Therefore, he argues that the foundations of a possible theory of "habitat fragmentation" should, in fact, lie in between independence and interdependence of habitat loss and habitat fragmentation. For this reason, observational studies of habitat fragmentation usually present habitat loss associated with the fragmentation process and these last effects must be removed by statistical techniques in order to isolate the effects of different habitat configurations comparing landscapes with equal HA [9, 10, 13].

The debate of the effects of spatial distributions of habitat in landscapes actually traces back to 1970s and 80s, when the ecology community wondered if one single large natural reserve has the same ecological value as several smaller reserves whose areas sum to that of the large reserve. The question "single large or several small?", referred to as SLOSS, which seemed simple enough, generated one of the most heated debates in the field of conservation ecology, with persuasive arguments by both sides for almost half a century. The viability of either approach, turns out, depends on the circumstances and specially the extinction risk of each species [14]. Overall, it has been preferable to argue for the habitat integrity and security of a single larger reserve for species conservation purposes [14, 15, 16]. Although the SLOSS debate did not lead to any general conclusions, it did pave the way for the current issues of habitat fragmentation in spatial and conservation ecology.

Fahrig (2003) [9] summarizes some years of debate on "what does 'several small' mean?", citing different observational studies which measured habitat fragmentation differently and, therefore, drew different conclusions about its effects. In short, in order to quantify habitat fragmentation effects on ecological responses, she stressed the importance of precisely defining the concept of fragmentation in the first place, which had not yet been settled in the ecology community and, up to this day, is still an "umbrella concept" for habitat configuration in general. In that classical review, Fahrig defines fragmentation as the result of the *fragmentation process* that causes "(a) reduction in habitat amount, (b) increase in the number of habitat patches, (c) decrease in sizes of habitat patches, and (d) increase in isolation of patches". The concept of degree of fragmentation was also introduced, measuring it in a continuous manner through a particular set of *fragmentation metrics*, which would be the quantification illustrated as a new dimension of landscapes in Fig.1.1(b). Moreover, the set of metrics in different studies and how they are

correlated among themselves and HA are highly debatable in the literature, which makes it quite hard to establish any general pattern in the ecological responses of fragmentation because different authors measured fragmentation in different ways and, as consequence, they draw different conclusions regarding both the magnitude and direction of these effects [9, 10].

From theoretical perspectives, the effects of habitat fragmentation have been studied under the lights of metapopulation persistence and networks of patches [17, 18], but these models abstract the properties of landscapes, making it hard to quantify the effects of fragmentation with measurable features of landscape, as fragmentation metrics. Other authors studied the effects of fragmentation on metapopulation persistence in spatially explicit model of fractal landscapes [12, 19]. Models that consider population dynamics, on the other hand, typically consider heterogeneous spaces to be periodic and/or smooth whereas the fragmentation patterns usually break the smoothness and regularity of landscapes [20]. Also studies of heterogeneity effects are commonly applied to uni-dimensional habitat intervals where the notion of fragmentation falls apart [21].

Therefore, we explore a model that describes single species distribution on landscapes considering different behaviour and diffusive movement across the landscape. Hence, demographic effects of habitat amount and fragmentation take place simultaneously in the spatial dynamics of species influenced by the landscape. The result is the emergence of effects of patch size, isolation, shape, edge and matrix use of landscape on a single species population. We employ this model of reaction-diffusion equations to generate synthetic data on single species distributions on artificially generated landscapes and afterwards we relate geographical properties of these landscapes to its ecological properties using statistical models.

In this work, we start introducing the mathematical model of partial differential equations in binary landscapes employed to generate the synthetic data in which we investigate the emergent effects of HA and fragmentation in the total population in landscapes. We find non-negligible effects of *fragmentation per se* and discuss the importance of matrix hostility to the direction of these effects. Lastly, we contrast effects of fragmentation considering unconstrained effects of HA rather than the traditional linear hypothesis employed in observation data.

Chapter 2

Model and methods

In this work, we solve a model of two reaction-diffusion equations commonly employed in ecological studies presented in Section 2.1 on landscapes, whose regions are either good or bad for species. We will refer to these classes as *habitat* (or *patch*) and *matrix*, respectively, and the method to generate these artificial binary landscapes is introduced in Section 2.2.

Initially, we treat the degree of fragmentation as a binary feature rather than a continuum spectra. In other words, we simply classify landscapes as slightly or highly fragmented. In further analysis, we use the *fragmentation metrics* reported in Section 2.3 in order to quantify continuously the effects of *fragmentation per se* on the average population density on landscapes via statistical models described in Section 2.4.

2.1   Mathematical model

Models of reaction-diffusion equations are a very large and general class of models that have been used to study chemical, ecological and geological problems, among others [22, 23]. Here, we discuss them in the context of ecological problems.

Our model consists in a bidimensional spatial domain, representing the landscape, which is divided in two regions: habitat (or, patch) and matrix. We are interested in the population distribution $u(x, y, t)$ of a singles species on this landscape in the stationary regime ($t \to \infty$). In our model, we set different growth terms in the different regions: in points belonging to habitat, the population grows logistically and diffuses, while in points belonging to the matrix, population dies at constant rate and diffuses. Therefore, we have the following set of equations:

$$\frac{\partial u}{\partial t} = ru\left(1 - \frac{u}{K}\right) + D_P \nabla^2 u \qquad (2.1)$$

in habitat patches, and

$$\frac{\partial u}{\partial t} = -\mu u + D_M \nabla^2 u \tag{2.2}$$

in matrix regions.

In Eqs. (2.1) and (2.2), r is the intrinsic growth rate of species in habitat, K is the carrying capacity density of habitat, μ is the death rate of species in matrix, and D_P and D_M are the diffusion coefficients in habitat and matrix, respectively.

Describing movement of species as a diffusive movement is an approximation to the tendency behaviour of populations of several species to occupy equally a region in the lack of environmental heterogeneity. It can also be seen as population description of the random and independent movement of individuals in the absence of heterogeneity [24]. This modeling also implies that the intraspecific competition within habitat is local, i.e., it occurs at spatial scales much shorter than those associated to the diffusion process in patches.

In this work, we are interested in studying the stationary distribution of the system of Eqs. (2.1) and (2.2). With an adequate change of variables, i.e. re-scaling the variables to natural units of space, time and biomass of the system, we can write the stationary state as an algebraic problem of one free parameter and two equations, in habitat and matrix, respectively:

$$u(1 - u) + \nabla^2 u = 0 \quad \text{and} \quad -\kappa^2 u + \nabla^2 u = 0 \,. \tag{2.3}$$

In Eq. (2.3), we identified the free parameter as a measure of the *Matrix hostility* (κ), defined in terms of the original parameters as

$$\kappa = \sqrt{\frac{rD_M}{\mu D_P}} \,.$$

This parameter can also be seen from the point of view of characteristic scales of length (movement) in the problem. It can be interpreted as

$$\kappa = \sqrt{\frac{r/D_P}{\mu/D_M}} = \frac{L_P}{L_M} \,,$$

and therefore, the parameter κ identifies the ratio between a characteristic intra-patch movement length (L_P) and characteristic inter-patch movement length or matrix penetrability length (L_M).

2.1.1 Habitat-matrix interface conditions

We do not expect that population densities are continuous at the interfaces between patches and matrix. One can argue that because in more diffusive regions individuals move more, the population concentration decreases and hence, discontinuous diffusivities lead to discontinuous population distributions [25]. Therefore, for the interface between matrix and habitat we follow the boundary conditions proposed by Ovaskainen [26] and revisited by Maciel and Lutscher (2013) [25], and we impose the continuity of flux, i.e.,

$$D_P \nabla u|_{x^P} = -D_M \nabla u|_{x^M} \, , \tag{2.4}$$

at the boundaries between patches and matrix, and also the discontinuity modulated by diffusivities and directional preference α, i.e.

$$D_P u(x^P) = \left(\frac{\alpha}{1 - \alpha} \right) D_M u(x^M) \, . \tag{2.5}$$

We exploited the mathematical notation by denoting with x^P or x^M as the positions at the patch side and matrix side of interface. In the outermost boundary of landscapes, we establish zero flux, i.e., $\nabla u = 0$.

The parameter α can be seen as a probability of an individual moving from the edge of habitat to matrix. It can be employed to make transitions asymmetric at the interface, meaning it is more likely an individual at the matrix move towards the habitat than the contrary. In this work, we assume for simplicity symmetric movements at the interface by considering $\alpha = 1/2$, i.e., no preferred direction of movement at the interface between regions.

We study the total abundance of species on landscape and on habitat, given respectively by the following integrals,

$$\langle u \rangle_L = \frac{1}{A} \int_A u^*(x) d^2x \, ,$$

and

$$\langle u \rangle_P = \frac{1}{HA} \int_{HA} u^*(x) d^2x \, ,$$

where the integration regions are the total landscape area (A) in the first case, and only the habitat areas (HA) on the second. The super-script * indicates we are working with the stationary solution of this model and there is no dependence on time nor on initial distributions. More precisely, u^* is the algebraic solution of the

system of Eqs. (2.3) with the interface conditions of Eqs. (2.4) and (2.5).

2.2 Artificial landscapes

The artificial binary landscapes were generated using a clustering method in which either new habitat pixels are laid randomly next to previous habitat pixels considering only 4-neighbours or it initiates a new habitat patch (cluster) with a given probability, which is the parameter that controls for the degree of fragmentation of the landscape. This is similar to the work of Tischendorf and Fahrig (2000) [27], considering only two patch types.

The probabilities of starting a new patch are normalized with the number of habitat amount, and their average are 50 times greater in the highly fragmented group of landscapes than in the slightly fragmented, and therefore the average number of patches in highly fragmented landscapes is 220, while the same average is 4.2 in the slightly fragmented group - the visual effects of these landscapes can be seen in Fig. 2.1.

For each fixed habitat amount, ranging from 5% to 90% in 5% increments, we generated 50 different landscapes in each degree of fragmentation and results shown hereafter are averages and analysis over these 1700 landscapes.
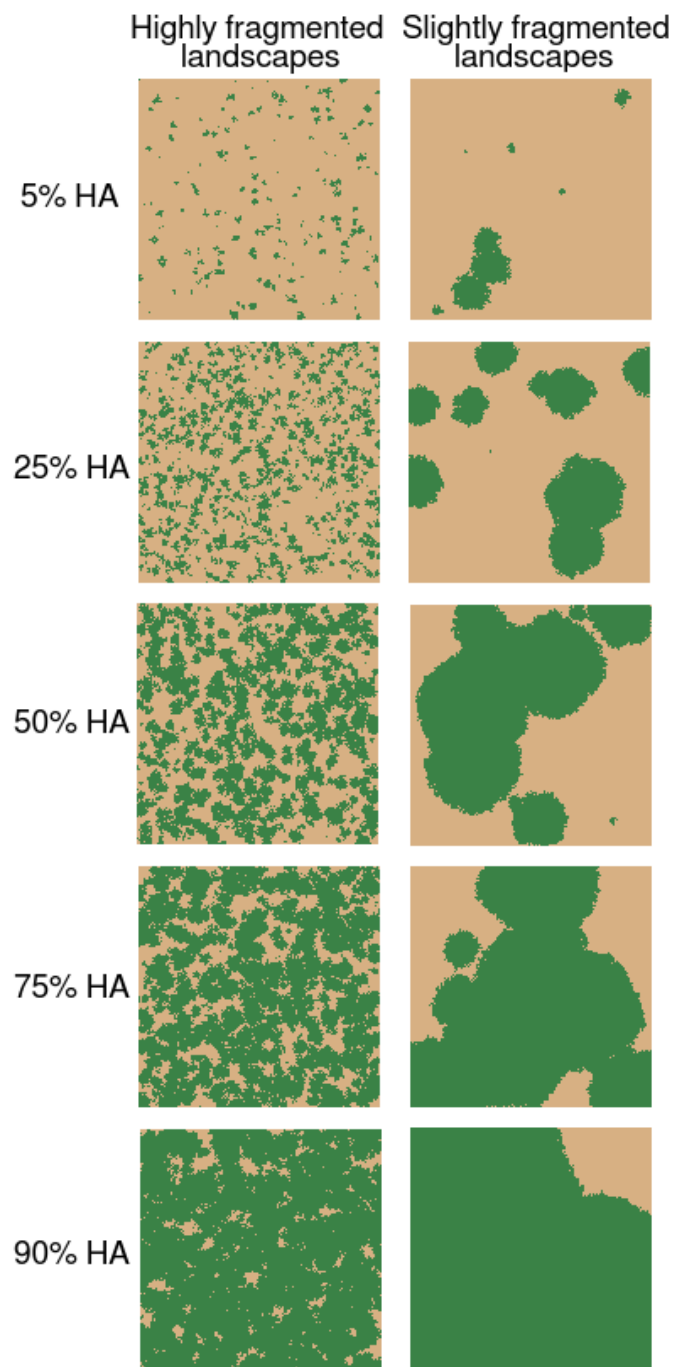
Figure 2.1: Examples of artificial landscapes in each group of fragmentation level. Left landscapes belong to the highly fragmented group, while right landscapes are in the slightly fragmented group. Rows indicate different habitat amounts (HA): 5%, 25%, 50%, 75% and 90%. In each row, landscapes differ by *fragmentation per se* .

2.3   Fragmentation metrics

Upon each landscape we calculated different fragmentation metrics as quantifications of different spatial aspects of the spatial distribution of habitat. In order to calculate metrics we utilized the package *landscapemetrics* [28] and employed the notion of 8-neighbours and edge-depth of 1 unit cell in landscape whenever necessary.

We calculated 29 fragmentation metrics available in the package and aggregated them in nine groups of redundant metrics (highly correlated), choosing one representative metric of each group, in preference to metrics commonly employed in the literature. We also established a selection criteria in order to use metrics that actually differentiate between slightly and highly fragmented landscapes and we only worked with fragmentation metrics whose difference between the averages of the highly and slightly fragmented landscapes were greater than 1 standard-deviation of the entire population, making sure that the fragmentation metric distinguishes these two large groups of landscapes, besides quantifying the fragmentation spectrum within each group. Therefore, we ended up with the fragmentation metrics listed below, considering different aspects of fragmentation, and hereafter represented by the short abbreviations in bold:

1. **NP**[1]: Number of Patches on the landscape. This is one of the most frequently employed metric in ecological studies.

2. **CAI**[2*]: Core Area Index, which measures the average percentage of core area of habitat in patches.

3. **MApP**[3*]: Mean Area per Patch on landscape.

4. **ED**[3]: total Edge Density on landscape.

5. **Gyrate**[4*]: average of the ratio between the perimeter of each patch and its hypothetical minimum perimeter.

6. **CircumsC**[4]: mean radius of Circumscribing Circles on each patch.

7. **PAratio**[4]: mean Perimeter-Area ratio over patches.

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*These fragmentation metrics are actually decreasing, on average, from the slightly fragmented to the highly fragmented landscapes. Therefore, high values of these metrics indicate less fragmented landscapes.

These metrics can be classified as representative of the following large group of metrics: (1) aggregation metrics, (2) core area metrics, (3) area and edge metrics and (4) shape metrics, in a classification proposed by McGarigal (2002) [29]. All metrics were calculated on the habitat class and are representative of the landscape features (therefore, averages over patches are not weighted by their areas).

In what follows, all fragmentation metrics were linearly normalized to vanishing mean and unitary standard-deviation across the 1700 landscapes. This allows us to compare the relative strengths of the different effects of landscapes aspects without bias of metrics sensitivity and variability.

When exploring the metrics distribution across landscapes we observed that the NP is very concentrated in close-to-zero values and presents a long tail. Therefore, we decided to work with order of magnitude of number of patches, namely $logNP$, that has a more compact distribution around its mean.

The seven final fragmentation metrics are weakly correlated with HA, $R^2 <$ 0.35, specially $R^2 < 0.1$ for ED, CAI, $CircumC$ and $PAratio$. Fragmentation metrics are correlated between themselves for a fixed HA ($R^2 > 0.5$).

2.4   Statistical models

With the descriptive models we propose to explain the influence of the predictor variables (geographical information) is related to average value of an Gaussian distribution of logits of the response variable, which in this case is the average population densities over the landscapes at three levels of matrix hostility. The logit function is the canonical linking function for the probability of binomial distributions, and hence the response variable can be interpreted as a probability to find an individual per space per time. We explore four models, synthesized in Table 2.1.

The proposed statistical model is equivalent to stating that the average population densities over landscapes follow a logit-normal distribution, in analogy with the log-normal distribution there is commonly applied in statistical studies of species abundance [30]. It is important to highlight that at several points of the analysis we focus on the direction of the effect of the predictor variables, and as the logit function is a strictly increasing function, it preserves the direction of effects of the various predictors.

Finally, as the solutions for stationary state of the equations of model, Eq. 2.3, were obtained numerically, they are restricted to the numerical precision employed,

Table 2.1: List and description of statistical models employed in order to relate geographical information of landscapes and the logit of the population density in the stationary state of the mathematical model

Model[a]	Description of Effects	Model formula[b]	Number of parameters[c]
1	Linear effects of HA and no effect of fragmentation	$a_0 + a_1 \cdot HA$	2
$2.F_j$	Linear and independent effects of HA and fragmentation metrics	$a_0 + a_1 \cdot HA + a_2 \cdot F_j$	3
$3.F_j$	Linear and interdependent effects of HA and fragmentation metrics	$a_0 + a_1 \cdot HA + (a_2 + a_3 \cdot HA) \cdot F_j$	4
$4.F_j$	Linear effects of *fragmentation per se*	$a_0^{(k)} + a_2^{(k)} \cdot F_j$	34[d]

[a] F_j represents each fragmentation metric, hence Models 2-4 are families of seven similar models.

[b] for the mean value of a Gaussian distribution of logits of the average population density on landscape.

[c] for the mean value of models. The constant variance is also another free parameter in all models.

[d] equivalent to 17 independent fittings on groups of 100 landscapes of constant HA, where the superscript (k) designates the group.

$1 \cdot 10^{-6}$. Thus, any value corresponding to a logit outside the range $[-10, 10]$ will also be considered as either one of the extreme values of the interval, since they are numerically indistinguishable.

In the equations for the mean value of the statistical distributions in Table 2.1, it is possible to notice the nestedness of Models 1, 2 and 3. Also, it is important to note that, mathematically, it is not possible to differentiate an increase (or decrease) in the effects of fragmentation metrics by HA from the increase (or decrease) in the effects of HA by the degree of fragmentation, since in both cases the quadratic term of interdependence is identical in Model 3. This interpretation is, hence, the result of the landscape ecology literature that stresses HA as the main component of the landscape [11].

Throughout all models we analysed, the variance of the Gaussian distributions are constant, assuming an homoscedastic response variable, and coefficients were estimated by the Maximum Likelihood Estimator (LME) method.

Chapter 3

Results

We start by presenting a visual inspection of the results contrasting the averages over the two large groups of fragmented landscapes - highly and slightly fragmented - in Section 3.1. This will provide insights to move afterwards to a quantitative analysis presented in Section 3.2, where effects of the various fragmentation metrics are tested in the statistical models, comparing continuously several aspects of the spatial distribution of habitat with synthetic data from 1700 different landscapes.

3.1 Contrasting highly and slightly fragmented landscapes

On the top rows of Fig. 3.1, we show the stationary population density averaged over the landscapes ($\langle u \rangle_L$) within each fragmentation degree group and on the bottom rows, the population densities averaged only over the habitat regions of each landscape ($\langle u \rangle_P$) as a function of the matrix hostility (κ), which is the only free parameter of the model. Different columns display five different total habitat amounts (HA from 80% to 5%), kept fixed in landscapes to guarantee that the differences observed in the two lines are due to the effects of *fragmentation per se* when considering populations with minimal mechanisms of diffusive movement and local reaction.

One can observe that the differences between highly and slightly fragmented landscapes can be in favour of either landscape group depending on the quality of the matrix between habitat patches. For low values of κ (roughly less than 1), representing soft (or mild) matrices which allow high matrix penetrability and inter-patch movement of species across the landscape, then *fragmentation per se* showed positive effects because it decreases the distances between the smaller patches and permit greater total populations in the landscape (blue curves above red curves in Fig. 3.1) and fairly similar occupations in habitat regions. In
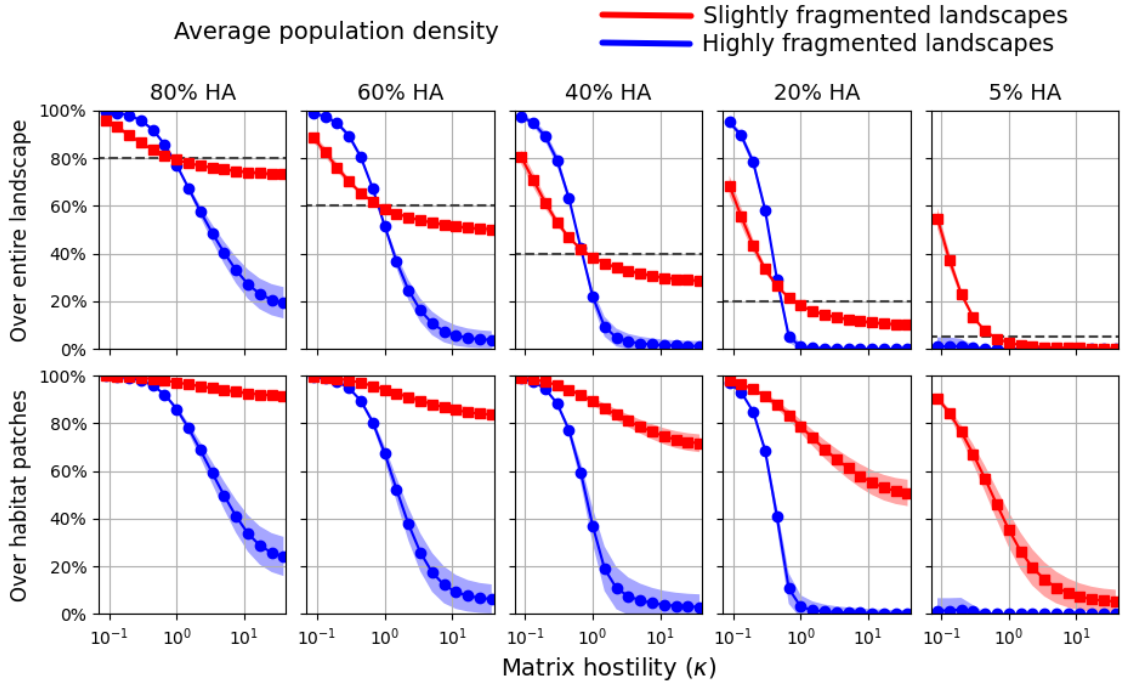
Figure 3.1: Top rows show mean total population in landscapes normalized by total area, $\langle u \rangle_L$, as a function of the matrix hostility (κ) in log-scale. Bottom rows display total population in habitat regions normalized by total habitat area, $\langle u \rangle_P$, as a function of the same variable as previously. Blue lines with rounded points display the averages over the highly fragmented landscapes. Red lines with squared points show the averages over sightly fragmented landscapes. Shade regions represent one standard deviation from mean value (50 landscapes in each group and HA were considered). Landscapes have from 80 to 5% of habitat amount in different columns, also shown in horizontal dashed lines within plots.

fact, fragmentation increases the total area of presence of population, ultimately decreasing the intraspecific competition within habitat patches. Thus, because the "effective area" where species can be found has been extended, such configurations allow larger total populations than in the case of slightly fragmented landscapes.

This conclusion is clearer when observing the the patterns of high and low density points on the spatial distribution of the stationary solution for six different values of matrix hostility and two examples of artificial landscapes, as shown in the schema of Fig. 3.2. Due to the fact that slightly fragmented landscapes have portions of habitat distributed less evenly, points in matrix far from habitat patches experience lower presence of species (see for instance the top-left corner of the middle row for $\kappa = 0.1$ of Fig. 3.2).

When it comes to weakly communicating patches, i.e. connected by a hostile matrix - high values of κ, roughly more than 1 - in which species cannot pene-
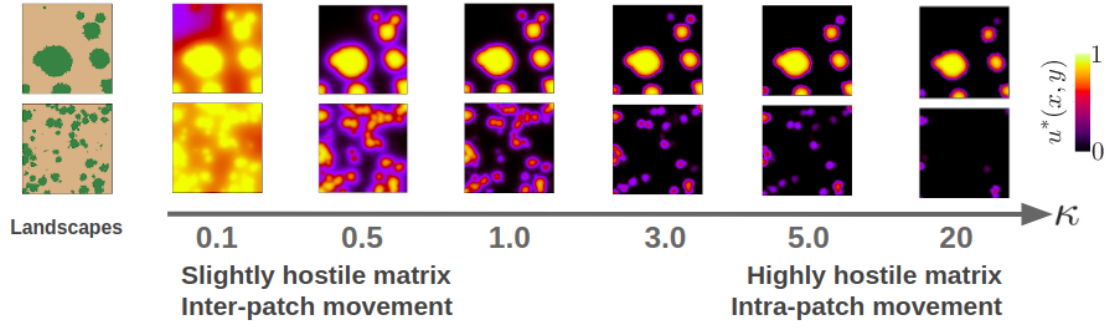
Figure 3.2: In the first column, two landscapes with 25% of habitat amount and different spatial configurations (slightly fragmented on the top row and highly fragmented on the bottom row). The following columns show the stationary solutions $u^*(x,y)$ in each landscapes for five values of matrix hostility κ. Low values of κ indicate soft matrices, while greater values of κ indicate highly hostile matrices. We propose to understand the solutions in terms of movement of populations: in soft matrix populations can migrate from one habitat patch to other (inter-patch movement) and the relevant features of landscape is the distribution of habitat though the landscape. On the other hand, the movement is confined in one patch in highly hostile matrices (intra-patch movement), and therefore the relevant geographical features of landscapes are core area.

trate, fragmentation led to extinction of species in smaller isolated patches and, consequently, to an overall reduction of species abundance with the degree of *fragmentation per se* increased, as seen in Fig. 3.2. Because hostile matrices do not allow inter-patch movement, high fragmentation can also lead to extinction for a hostile enough matrix, specially in lower HA when larger intervals of extinction occurred, simply because no patch alone can sustain the population due to the critical patch size of reaction-diffusion equations [26]. In the schema of Fig. 3.2, one can observe that the relevant qualitative ecological features of landscapes in hostile matrices is core habitat area, rather than simply habitat area.

In Fig. 3.3, we show the curve of $\langle u \rangle_L$ for slightly fragmented landscapes in hostile matrices as a function of the HA in order to test the hypothesis that the central feature is core area rather than total area of habitat. In dashed gray line, we propose a model linearly proportional to habitat area, respecting the relations of extinction when there is no habitat on landscape and complete occupation on a full-habitat landscape; whereas in the black dashed line we propose the following relation

$$\langle u \rangle_L = HA - cHA(1 - HA) \,,$$

i.e., the habitat amount minus the average edge density as a function of HA. The constant c converts edge density to its ecological effect on the population and it is fitted in points on graph as $c = 0.42$. Fig. 3.3 shows that the correction of the
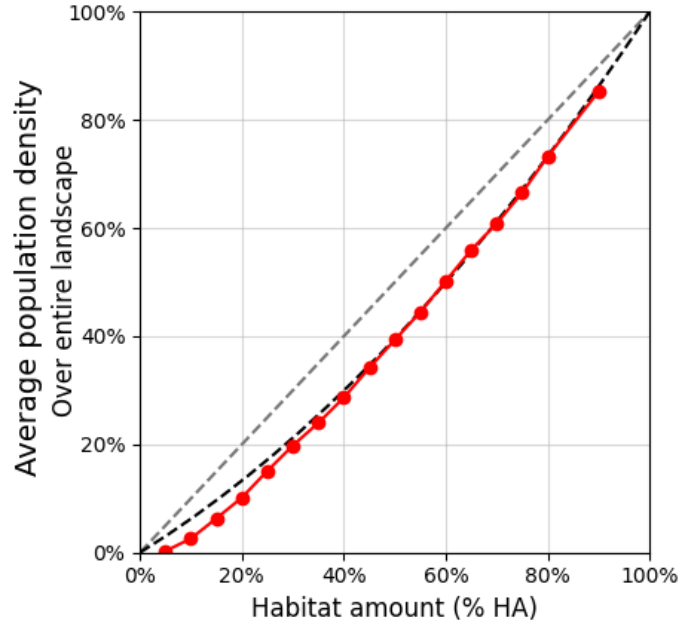
Figure 3.3: Average population density over entire landscape, $\langle u \rangle_L$, of slightly fragmented landscapes on hostile matrices. Grey line is linearly proportional to Habitat Area (constant carrying capacity density hypothesis). Black line is proportional to Cora area, i.e., subtracting the typical edge density of the habitat amount.

effects of core area in the abundance-HA relation seems to well explain the shape of the curve drew from synthetic data.

Variations in average population density between landscapes in the same groups of level of fragmentation and HA, shown in Fig. 3.1 as a colored shadow region with one standard deviation from the mean value, are not uniform in the habitat amount gradient. For instance in high HA, the variations of population density are higher among highly fragmented landscapes than slightly fragmented landscapes, specially in hostile matrices. And on the other hand, considering low HA, the opposite is true because in this same regime the highly fragmented landscapes led to extinction of populations.

3.2 Statistical description of synthetic data

Now we compare statistical models to investigate hypothesis to explain the data generated from the solutions of Eq. 2.3 on top of 1700 different landscapes for three levels of matrix hostility - soft ($\kappa = 0.08$), intermediate ($\kappa = 1.00$) and hostile ($\kappa = 38.00$) - in order to quantify the effects of different fragmentation metrics, which continuously order landscapes according to one aspect of their

fragmentation degree.

We applied the different models described in Table 2.1 to statistically explain the average population density with predictor variables of HA and one of seven fragmentation metrics, and also testing hypothesis about their inter-dependency. Finally, we compared the models directly by their relative-likelihood, since the number of parameters in each model (between 2 and 4 parameters) are insignificant compared to the data size (1700 different landscapes).

### 3.2.1 Testing the Habitat Amount Hypothesis on landscape level

The Habitat Amount Hypothesis (HAH) is an empirical hypothesis that concerns the relation between the ecological value of a landscape, more particularly addressed by density of species per patch, and the total habitat amount surrounding this focal patch. It can be stated in four points [31]: (1) the density of species per patch is more strongly and positively correlated with HA surrounding the focal patch than its size or isolation; (2) the HA is better predictor of species density than the size of the patch or isolation combined; (3) there is no effect of habitat fragmentation (*per se*) on species density; and finally, (4) the effects of patch size and isolation do not vary along the gradient of HA.

In Fig. 3.4, we show the results of Model 1, which includes HA as the only predictor variable to explain the average densities across landscapes for the three cases of matrix quality considered in this study. We can observe positive effects of HA on the average population density, as well as greater variances in the response variable at lower HA, specially in more hostile matrices.

In fact, we observed that all models, 1, 2 and 3, presented positive effects of the HA on population densities, i.e., larger portions of habitat allow for greater population densities, as seen in Fig. 3.5, agreeing with the current landscape ecology literature [11]. In the cases of intermediate and hostile matrices, habitat loss is also related to an extinction threshold, i.e. a critical value which below HA does not permit populations to settle (or permit very small populations susceptible to stochastic effects).

Beyond observing whether the values of average population densities are distributed around the predicted mean of the Gaussian distribution (Blue line of Fig. 3.4), one can also check if regions of points corresponding to different degrees of fragmentation are vertically distributed in soft and hostile matrices across the whole HA gradient. In intermediate matrices, high HA did present
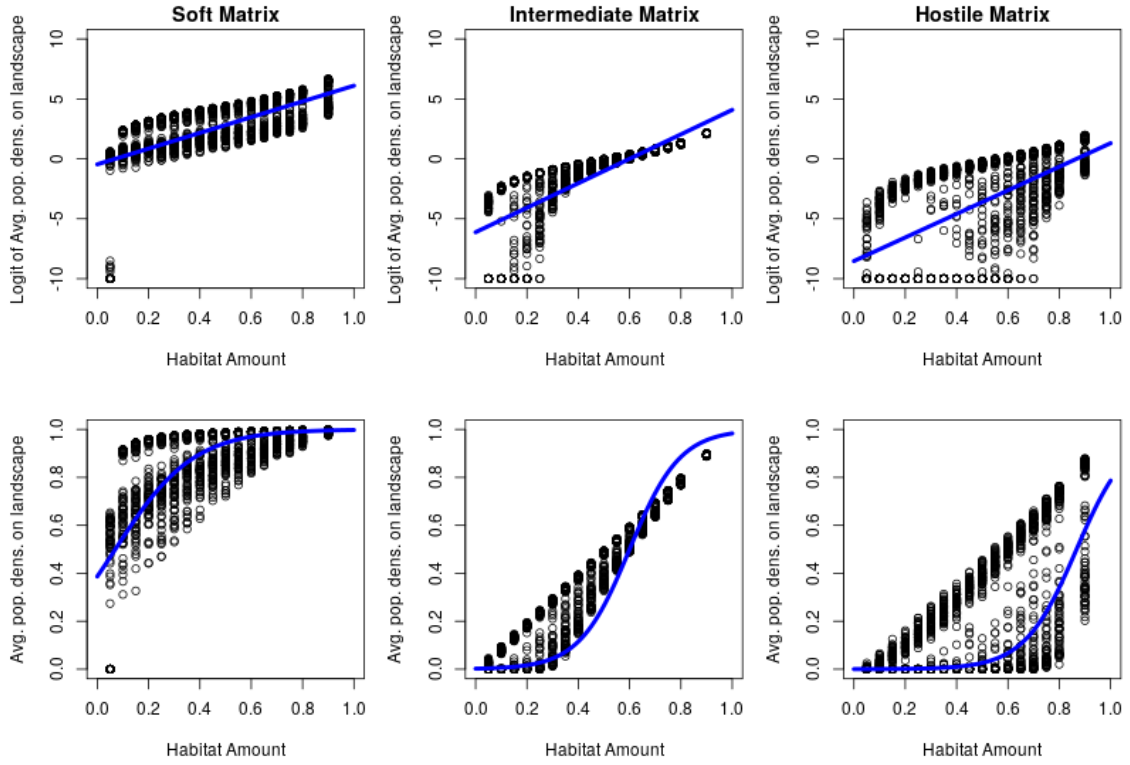
Figure 3.4: Fitting of Model 1 into the data from 1700 landscapes where the blue line represents the mean value of the Gaussian distribution of logits. Model 1 implies that the logits of average population densities are normally distributed with linear effects of HA in the mean value and constant variance. In the top row are the fittings in logit densities and in the bottom row the same fittings in linear scale of densities. The columns indicate the quality of the matrices: soft, intermediate and hostile, from left to right.

significant variations. In fact, recent confrontations of the HAH by theoretical [32] and observational [33] perspectives suggested that fragmentation effects are relevant when it comes to determining the ecological value of landscapes, and its importance varies across the gradient of habitat amount.

In order to confront the HAH, represented by Model 1, with models that include the effects of fragmentation (Models 2 and 3) in our synthetic data, Fig. 3.6 shows the Relative Negative Log-Likelihoods between the Model 1 (only effects of HA), Models 2 (independent effects of HA and F_j) and Models 3 (interdependent effects of HA and F_j, see Table 2.1) at the three matrix hostilities considered. Between the models we tested, the Likelihood Ratio Test (LRT) criteria states substantial support for Models 3.$logNP$ for soft and intermediate matrices and 3.ED for hostile matrices, as the best models to explain the observed data. Given the visual analysis explored on the previous section, it is not surprising that the most relevant aspects of fragmented landscape vary across the levels of matrix
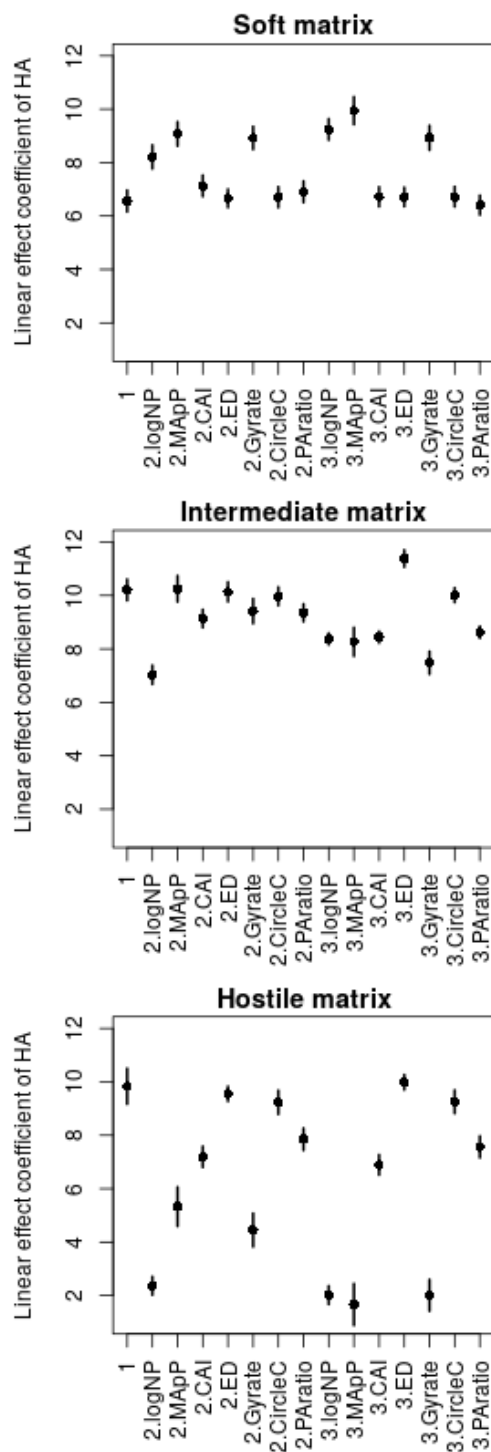
Figure 3.5: Comparison between the coefficients a_1 of the linear effect of the HA in the fitted Models 1, 2 and 3, considering different fragmentation metrics in Models 2 and 3. In all models, the effect of HA on the average population density is positive.

hostility.

Regarding the robustness of these model selections with respect to the criteria
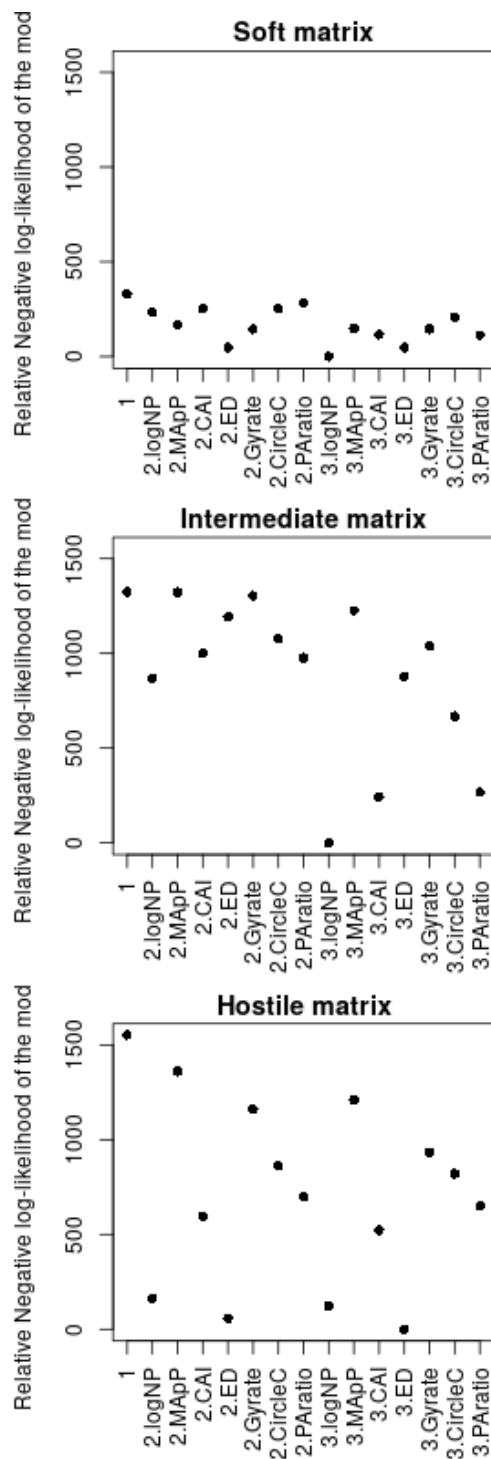
Figure 3.6: Comparison of the different Relative Negative Log-Likelihood (NLL) between Models 1, 2 and 3, considering different fragmentation metrics in Models 2 and 3. This selection criteria means that the synthetic data observed is more probable or plausible as given by the statistical model with the lowest NLL.

applied, the same models presented the minimum variances among all tested models, and also performed best according to both AIC and BIC information loss criterion. Therefore, considering populations with diffusive movement and local reactions in binary landscapes of habitat and matrix, we can conclude that synthetic data strongly supports the presence of non-negligible effects of fragmentation, in its several aspects, on the average value of single species abundance in these landscapes, in addition to effects of HA. More particularly, the model selection criterion points towards interdependent effects of HA and fragmentation, i.e., the effects of fragmentation are not homogeneous across the HA gradient.

It is important to realise that the HAH is formulated in a patch-centric view of ecological value, where a landscape is considered as a surrounding circular buffer around a focal patch sampled. Therefore, two key aspects to relate our model to HAH is to consider that we are working with landscape-scale effects and that we will deal with the effects of fragmentation on the average population density of a singles species on landscape rather than landscape richness. Because our artificially generated landscapes have similar fragmentation patterns across the entire landscape, we can fairly approximate the fragmentation around a patch with the landscape-level fragmentation. Also, our response variable belongs to a single species based on the premise that intraspecific abundances correlate with interspecific abundance (richness) [34, 35], and both can be used as metrics for a more abstract information, referred to as *ecological value* of a landscape.

3.2.2   The magnitude of the effects of fragmentation

In the previous section we have concluded that the degree of fragmentation, quantified in its several aspects by fragmentation metrics, have non-negligible effects on the ecological value of landscapes. Then now we can pose the question of what landscape aspect (or aspects) affects it the most and therefore should be considered when choosing fragmentation metrics for observational studies.

We can directly compare the linear coefficients of the fragmentation metrics in each model because all fragmentation metrics are measured with respect to their standard-deviation across all landscapes, and hence coefficients are dimensionless. We present the coefficients of the fragmentation metrics in Models 2 (a_2) and Models 3 ($a_2 + a_3 \cdot HA$) in Fig. 3.7 for each matrix hostility considered.

The conclusions that can be drawn from coefficients of Models 2 (black dots of Fig. 3.7) are that when considering the effects of fragmentation independent
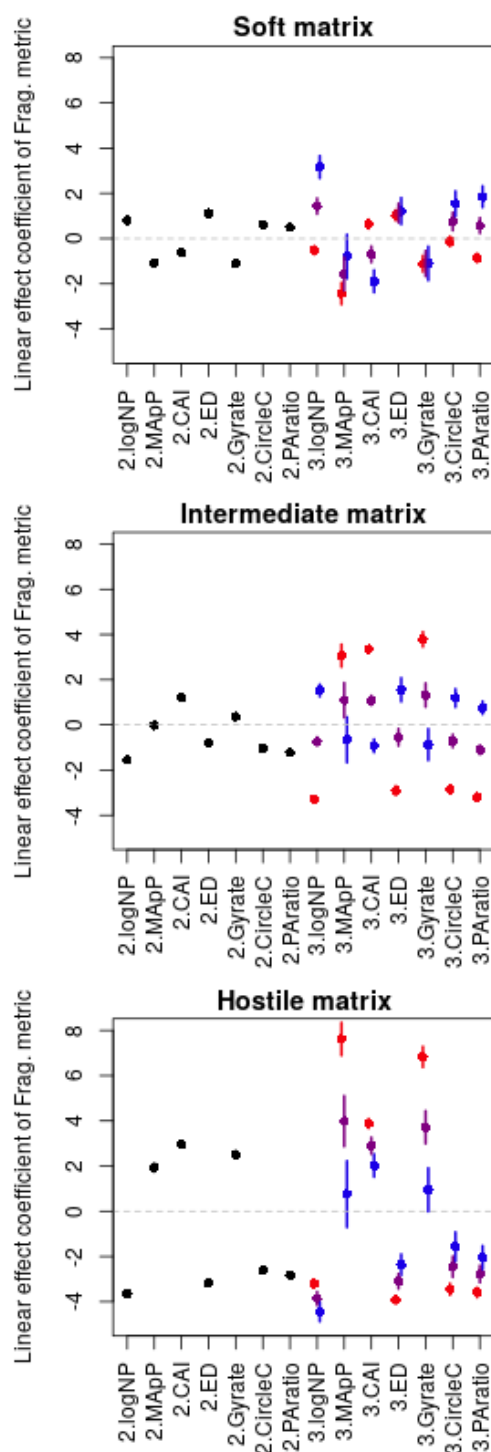
Figure 3.7: Comparison between the coefficients a_2 of the linear effect of fragmentation metrics (scaled in units of their standard deviations) in Models 2 and 3. In Models 3 the coefficient varies linearly across habitat amount (HA) gradient, given by $a_2 + a_3 \cdot HA$ in the model, therefore it is represented in the Figure for $HA = 5\%$ in red, $HA = 50\%$ in purple and $HA = 90\%$ in blue.

of the effects of HA, then the magnitude of these effects were non-vanishing in all scenarios of hostility and aspects of fragmentation, with a single exception in the case of $MApP$ in an intermediate matrix where $a_2 = 0$ is an equally plausible value in our canonical plausibility criterion (Relative log-likelihoods differences smaller than $\log(8)$). The intervals of plausibility of coefficients in Model 2 are lower than 20% of their magnitude and the MLE profiles are close to parabolic curves due to the high number of data.

In the family of Models 3, all metrics showed an inversion in the direction of the effects produced along the HA gradient on the average population density in the landscapes when considered an intermediate matrix. Whereas, in a soft matrix, the metrics of $logNP$, CAI, $CircumsCircle$ and $PAratio$ (4 of 7) inverted the direction of its effects, while the metrics of ED and $Gyrate$ did not suffer strong effects from the HA on their linear coefficients. For a hostile matrix, no metric changed the direction of its effect along the HA gradient, although for metrics $MApP$ and $Gyrate$, an inversion is equally plausible in within the canonical plausibility criteria (and in Fig. 3.7 we overestimate the total intervals of plausibility of the linear coefficient of the fragmentation metrics assuming independent relations between the intervals of plausibility of a_2 and a_3).

The direction of effects of different fragmentation metrics are opposite when contrasting opposite qualities of matrix, and they agree with the conclusions taken previously in the visual analysis of the average population densities - here, one must consider also if the metrics are increasing or decreasing with the degree of fragmentation, as indicated in the footnote of *Methods and models* section. This observation can be made by comparing the points of opposite sides of the dashed line in the first and last rows (soft and hostile matrices) of Fig. 3.7.

In general, the magnitude of the linear effects of the different fragmentation metrics on the logit of the average population density is of the same order of magnitude that the effects of HA, when the metrics are measured in terms of their standard deviation (see Figs. 3.5 and 3.7). When observing the linear effects of HA on the coefficients of the fragmentation metrics of soft and hostile matrices, in general fragmentation has greater effects in lower HA.

3.2.3 Comparing the effects of fragmentation and *fragmentation per se*

In Model 4, we are interested in verifying the robustness of the direction of effects of fragmentation metrics within the HA groups (with respect to their effects on the totality of 1700 landscapes), in order to remove the correlations between fragmentation and HA which can lead to different conclusions about the direction of the effect of fragmentation metrics, as pointed out by several authors (see [10, 36]) and is exemplified by Fig. 3.8, which shows a case of *Simpson's paradox* for correlated data sets. In the type of data studied, landscapes with smaller HA tend to be more fragmented, reflecting correlations between HA and fragmentation metrics, which is one of the main arguments used when addressing these effects from observational data-sets.

The difference between the effects of fragmentation over these two different groups of landscapes would be the fundamental distinction between the effects of *fragmentation per se* and fragmentation, i.e. controlling or not controlling the HA. Typically in literature, the effects of HA are supposed linear and removed from
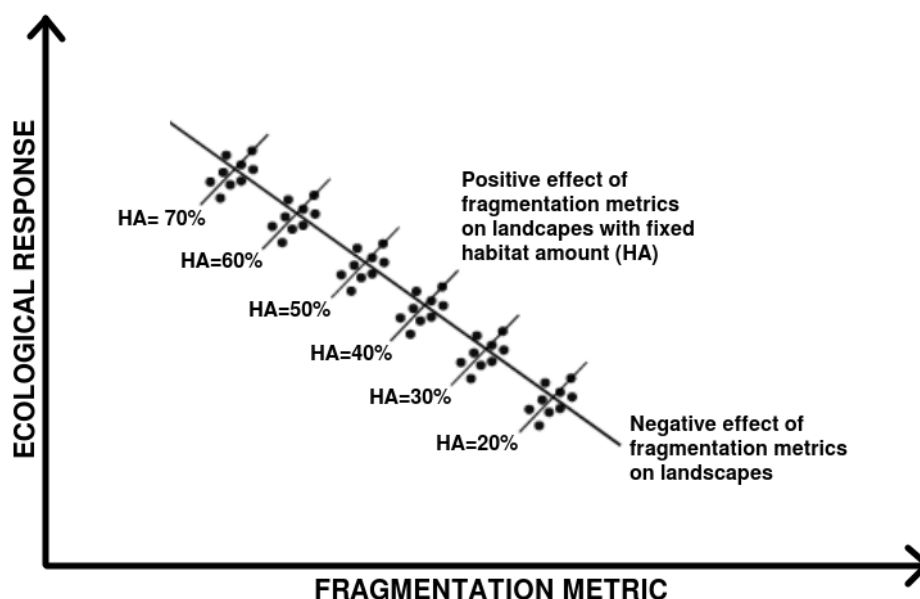
Figure 3.8: Example of *Simpson's Paradox*, where correlated variables can bring dubious conclusions on their effects, particularly exemplified in the context of habitat fragmentation, where landscapes with smaller HA tend, in general, to be more fragmented. The direction of effects of fragmentation metrics on the ecological response of landscapes can be opposed if there is no control over the HA in landscapes. This is the fundamental difference between fragmentation and *fragmentation per se* addressed by several authors.

the statistical analysis by employing Linear Mixed Effect Models (LMEM) since in observational studies it is often impossible to find a set of landscapes that differ exclusively by the degree of fragmentation [33, 31].

In the left and right columns of Fig. 3.9, it is possible to compare the different coefficients for the best two fragmentation metrics according to previous results of model selection, namely ED and $logNP$, respectively. The figure shows the coefficients of Model 3, which considers a joint linear effect of the HA and fragmentation (in red) and the coefficients of effects of *fragmentation per se* across HA gradient in Model 4 (in black). The later considers the effects of the fragmentation metric within each cluster of HA without any assumption on the effects of HA - what we will refer to as the "effect of *fragmentation per se* " on population densities.

We notice two distinct nonlinear patterns in the effects of fragmentation metrics across the HA gradient when there is no restriction of effects of HA: (i) parabolic behaviour where the effects are more pronounced for middle habitat amounts, as in the case of $logNP$ in hostile matrices and (ii) in the intermediate matrix, the effects of *fragmentation per se* occur especially below the threshold of 30% in both metrics, since higher HA showed much smaller linear coefficients of the *fragmentation per se* effect on the logit of average population density.

The first non-linear pattern could be explained in terms of the variability of the fragmentation metrics in each 50-landscape group of fixed HA. Some fragmentation metrics, as the ED, have a parabolic shape in the HA gradient due to their symmetry with respect to habitat and matrix [9]. Hence, because metrics reach its maximum average value at $HA = 50\%$, it would correspond to registering the lowest values of its coefficient in the HA gradient. The distribution of $logNP$ is not parabolic in the HA gradient and therefore the parabolic pattern of its effects cannot be understood under the same assumption.

The second non-linear pattern of the effects of *fragmentation per se* presented in the intermediate matrices can be easily observed on data points in Fig. 3.4, where at high and medium HA, there is a very small variance around the mean value, representing the absence of fragmentation effects in landscapes with intermediate matrices. Furthermore, it also explains why all fragmentation metrics inverted the direction of their effects across the HA gradient in Model 3 for an intermediate matrix (Fig. 3.7).

Overall, for soft and hostile matrices, the linear effects of fragmentation and *fragmentation per se* on the logit of average population densities agreed in direction, despite different intensities and patterns across groups of landscapes with different

HA. In other words, we conclude we have not perceived the effect of Simpson's paradox on our analysis, and linearly suppressing the effects of HA in synthetic data produces fragmentation effects that qualitatively reproduce the effects of *fragmentation per se* on species abundance.
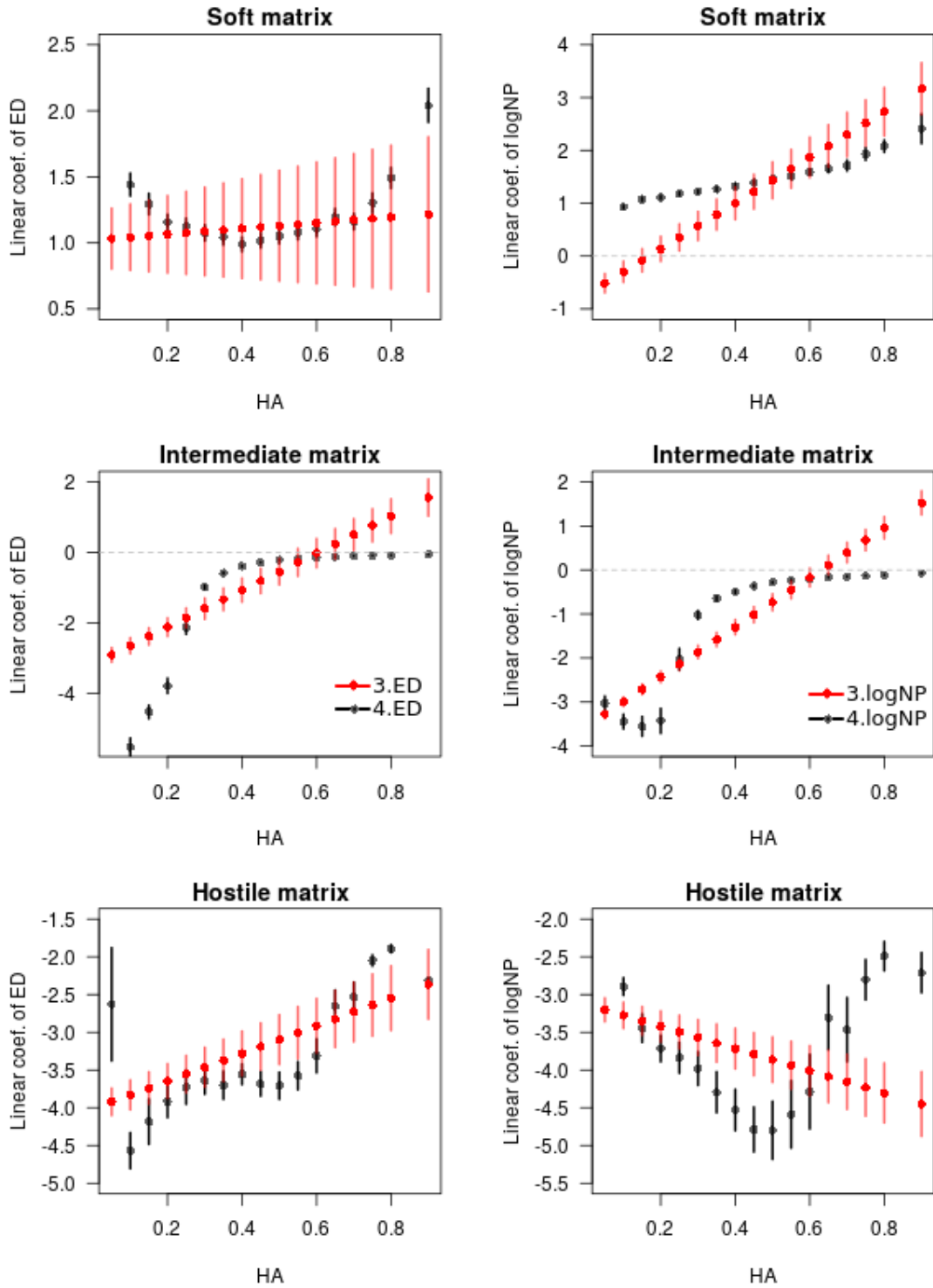
Figure 3.9: In the left column, comparison between the linear coefficients of the effect of fragmentation measure by Edge Density (ED) in Models 4.ED in black ($a_2^{(k)}$ - effect of *fragmentation per se*) and 3.ED in red ($a_2 + a_3 \cdot HA$ - effect supposing a linear variation across the HA gradient). In the right column, same comparison with $logNP$ as fragmentation metrics.

Chapter 4

Discussion

It is already well established that habitat loss leads to negative ecological responses both from observations and also several mechanisms that act simultaneously in detriment of species. Habitat loss decreases the reproduction rate and breeding success rate, reduces the trophic chains length, the number of specialists and large-bodied species and diminishes the dispersal success, predation rate and foraging success rate [9, 11]. Also, habitat loss impacts negatively the biodiversity because not only regions with less habitat contain a subset of the species found in landscapes with more habitat (i.e., passive sampling), but also because the ecological processes are affected by habitat loss and isolation in an ecosystem decay phenomena [37]. In the model we analysed, habitat amount present positive effects to the abundance of single species in all cases (Fig. 3.4), meaning that habitat loss was prejudicial to the average population density on landscapes.

Our model presented one single parameter to characterize the stationary state solution, represented by κ, interpreted as the hostility of the matrix, and it can be related to the ratio of intra to interpatch movement (or matrix penetrability), or diffusive coefficients and reaction rates in habitat and matrix. This parameter ended up being fundamental to the qualitative and quantitative descriptions of the effects of habitat fragmentation to the average population density in our results and, therefore, the model analysed suggests that there should be a fourth axis of complexity to the plot of Fig. 1.1(b), independent of the others: matrix hostility (or its inverse, matrix quality).

Matrix hostility has been employed as a *fragmentation metrics* by some authors who claim that more hostile matrices induce greater isolation between patches [10]. It is true that in our model the matrix hostility κ alters the isolation and communication between patches, nevertheless the effects of high and slight fragmentation on landscapes were dependent of matrix hostility, showing these quantifications are complementary but not redundant. Unifying the matrix hostility with patch size and isolation into one *effective patch isolation*, as proposed by Ricketts *et al.* (2001) [38], seems a reasonable option and could be further explored within this

framework.

As consequence, our results suggest that observational ecological studies designed to understand the effects of *fragmentation per se* should control for both total habitat amount on landscape as well as the matrix hostility. The variable direction and magnitude of the effects of *fragmentation per se* when considering diffusive movement and local reaction could explain, at least in part, the collection of conflicting findings in observational studies and proposed mechanisms [13, 36, 39, 40, 41, 42]. For instance, Fahrig (2017) [13] recently reviewed the observational studies on the effects of *fragmentation per se* in experiments or observations of singles species (Fig.9(d) in [13]) concluding 74 (32%) presented significant negative effects while 158 (68%) studies showed significant positive effects.

Our model points towards avoiding the generalization of effects of *fragmentation per se* when considering observational studies, and rather searching for common patterns considering different matrix hostilities and taxa. For instance, there is good empirical support for matrix use and presence as an important predictor to species sensitivity to fragmentation, specially among habitat specialist species [43], where our binary description of the landscapes should work the best. Although, it must be mentioned that a few composed measures of the degree of specialization of species use metrics of matrix use and presence, turning this argument into a cyclic reasoning, as pointed out by Henle *et al.* (2004) [39], who also noted the correlation between matrix use/presence and dispersal movement, i.e., inter-patch movement, as also observed in our results.

In a soft matrix, we observed that highly fragmented landscapes induce a larger communication between the smaller and less isolated patches, increasing the area of presence of species and reducing, therefore, the intraspecific competition within habitat patches, leading to overall larger populations than slightly fragmented landscapes. This argument appeared as the main explanation by observational studies to reason for positive effects of *fragmentation per se* in the meta-analysis of Fahrig (2017) [13], and the intraspecific competition release was also a frequently cited explanation. Additionally, empirical evidence has also been reviewed by Henle *et al.* (2004) [39], who found that species with greater mobility capacities in matrix, i.e. more matrix tolerant, can integrate several fragments into a home range and thus are less sensitive to moderate habitat loss and fragmentation than species that perceive matrix as more hostile. When several geographical patches are connected by biological processes of species, such as dispersion or genetic flow, they are said to form a *functional patch* [44, 45]. In our model, functional patches

connected by dispersive movement (inter-patch movement) are an emergent phenomenon, favored by the degree of fragmentation in soft matrices, ultimately increasing the functional connectivity of patches in landscape.

The quality of matrix becomes extremely important to the settlement of species on highly fragmented landscapes, as noticed in previous theoretical work for reaction-diffusion equations [46]. We observed extinction of species at low HA and high matrix hostility, as seen in Fig. 3.1 for HA lower than 30%. Its dependence on matrix quality happens because the critical patch length is an increasing function of κ, and in fact it can be derived analytically for uni-dimensional patches (Eq. (11) of [25]) and circular patches. In fact, the lower the HA the wider the range of matrix hostilities leading to extinction. For instance, species could not settle in highly fragmented landscapes for any matrix hostility considered in landscapes of 5% of HA.

Hence, our model proposes that for conservation of species the slightly fragmented landscapes show the presence of population in greater ranges of matrix hostilities than highly fragmented landscapes. Thus, slightly fragmented landscapes would be safer natural reserves. It is also worth mentioning that landscape management aiming to decrease matrix hostility can be an effective complement to habitat restoration in highly fragmented landscapes. Henle *et al.* (2004) [39] also found empirical evidence in literature that abundance/presence on matrix (matrix tolerance) is significantly negatively correlated with the tendency for extinction when considered separately in statistical models for species sensitivity to habitat fragmentation.

In slightly fragmented landscapes on the other hand, the distances between neighbor patches are greater and they are less uniformly distributed across the landscape. We observed that in soft matrices it decreases the total abundance on landscape because greater distances led to a decrease of the patch communication, although the total abundances on habitat patches are pretty similar to the ones on the highly fragmented landscapes. Greater values of core-area of habitat patches on slightly fragmented landscapes made the species settlement possible even when there was no inter-patch communication (high hostility). Species extinction were observed in slightly fragmented landscapes at extremely low HA, such as 5%.

The effects of *fragmentation per se* on the ecological value of landscapes have been discussed extensively in terms of species abundance and matrix hostility, both theoretically and experimentally. For instance, Palmeirim *et al.* (2019) [36] reports

that the abundance of 3 out of 20 species of small mammals considered increased with fragmentation metrics in the Atlantic Forest, while other four species had an inverse relationship. This pattern could fit into our model as a distribution of different matrix mobilities experienced by different species. Also, van der Hoek *et al.* (2015) [40] studied the extinction probability of forest-breeding species and its variations with habitat amount and degree of fragmentation, concluding that the effects of fragmentation vary between species, across different locations and across the gradient of HA. From a modelling viewpoint, Roque and Chekroun (2010) [47] also found different directions for the effects of fragmentation depending on the dispersal ability of species in a harvesting scenario.

It also has been suggested in the literature that fragmentation effects, such as patch size or isolation are less significant (some authors even say that they are "negligible") than habitat loss impacts on ecological responses throughout the whole HA gradient [13, 42]. These claims are also part of the Habitat Amount Hypothesis (HAH), recently debated by analysis of sets of data [33, 31]. For instance, concerning theoretical studies, it was found that even idealised settings with synthetic data cannot easily get significant support or refutation for the HAH when following the tests outlined by Fahrig (2013) [32].

The recent work of Püttker *et al.* (2020) [33] has also questioned the HAH from an empirical perspective. They applied hierarchical models, namely Linear Mixed Effects Models (LMMs), to several data-sets of richness of species in different landscapes in Atlantic Forest with different forest covers (habitat amounts) and different fragmentation degrees. They found: (i) highly fragmented landscapes, which results in higher edge densities, diminish significantly number of species, regardless of forest cover, but specially in intermediate forest cover; (ii) forest fragmentation should have detectable impacts on species even in higher forest covers; and (iii) the effects of habitat fragmentation vary in strength and direction (i.e., either positive or negative) along the gradient of habitat amount. They analyse results using intervals of habitat amount in which the fragmentation metrics employed, number of patches (NP) and edge density (ED), correlate to forest cover non-monotonically because both metrics grow for small habitat amounts and decreases for high habitat amounts [9]. Hence, assuming linear effects of both HA and fragmentation metrics may have led to distortions on their analysis. Later work analyses the same type of data but from a patch-scale studies, i.e. considering a landscape buffer surrounding an sampling point (or points), and reported results in agreement with HAH [31].

Our results support that the linear coefficients of the effects of fragmentation metrics when measured with respect to their standard-deviation (hence re-scaled to unity, typically between -1 and 2) are, in fact, of the same order of magnitude of the effects of HA (between 0.05 and 0.9) when supposing linear effects on the mean value of the logit of species density on landscapes. Furthermore, when the effects of fragmentation metrics can vary on the HA gradient, then the effects are accentuated at low HA.

Although we are using landscape fragmentation and ecological responses to confront the HAH, we argue that in artificially generated data the fragmentation patterns are uniform across the entire landscape, and therefore it can be seen as a reasonable approximation of the patch-scale fragmentation and ecological responses because these two scales are correlated. Moreover, this model can be easily adapted to extract patch-centric geographical and ecological information at different characteristic radii of the focus patch in order to establish the most significant spatial scales of measurement of both fragmentation metrics to ecological responses.

The direction of the effects of fragmentation were robust with respect to the fragmentation metric employed to continuously order the degree of fragmentation of landscapes. Several model selection criteria pointed towards metrics of number of patches, $logNP$, and edge density, ED, as the best predictor variables. The robustness of effects of fragmentation regarding the choice of fragmentation metric is important because they measure different aspects of the landscapes and in addition they correlate differently with HA [9], validating that conclusions surpass possible correlation problems. Fragmentation metrics are highly correlated for a fixed HA because the method employed to generate random landscapes explores one pattern of fragmentation with typically circular patches (or merges of those). Because binary landscapes are very elementary, we don't expect different generating methods to alter the qualitative findings, although the quantitative analyses can be sensitive to changes in the correlations between metrics.

We still have to learn more about the fragmentation metrics and general characteristics of real-world landscapes to be able to infer the geographical features of them that have the greatest ecological value of landscapes. When working with real landscapes, the patterns of fragmentation may not be homogeneous due to several mechanisms that accumulated to generate those patterns [20]. In addition, because such mechanisms fragmented landscapes in different spatial scales, another fundamental point regarding natural landscapes is discussing is the

typical scales at which fragmentation is measured. Using artificial landscapes, we could generate uniform fragmentation patterns across the landscape and robust patterns to changes in the size of landscapes. From qualitative results of this model in Fig. 3.2, we observed that the relevant characteristics of the distribution of habitat in landscapes to populations may vary depending on the matrix hostility. For instance, because soft matrices allow greater inter-patch communication, aggregation and isolation metrics seem to be good candidates to quantify fragmentation in landscapes with low matrix hostility. On the other hand, core-area metrics seem better candidates for hostile matrices, which do not allow interpatch communication and hence patches act isolated.

We also contrasted the coefficients of the effects of fragmentation metrics on all landscapes with its effect within groups of landscapes with fixed HA, ensuring our results consider only effects of *fragmentation per se* . When we contrast the results of effects of fragmentation metrics considering effects of HA linearly constrained (Model 3) or unconstrained (Model 4), then two non-linear patterns of intensity of the effects of *fragmentation per se* across the HA gradient were observed, while the direction of both effects are similar.

The first non-linear pattern of effects of *fragmentation per se* across the HA gradient is a parabolic effect, as seen in Fig. 3.9 for Edge density in soft matrix and $logNP$ in hostile matrix. This pattern can be explained by a greater variance of some fragmentation metrics for intermediate HA, such as ED, but it doesn't seem to be the case for $logNP$, where stronger effects peaked at $HA = 50\%$. The second pattern is significant effects restricted to low HA (typically $HA < 30\%$), as seen for intermediate matrices in Fig. 3.9, agreeing with previous theoretical models of metapopulations in patch networks, phenomena specially related to the percolation threshold of networks [48].

Usually studies on the effects of *fragmentation per se* are more focused on biodiversity than single species abundance. The extrapolation of abundance to richness has to be carefully taken given that multi-species systems show a variety of possible interactions and effects. Richness, i.e. the number of species in a landscape, is a subjective metric of ecological value. In fact, the "ecological value" cannot be quantified by a single number because it is a context-dependent quantity that incorporates several ecological aspects of ecosystems. The biodiversity of a landscape can hide subtle effects such as the invasion of non-native and generalist species, replacing native and specialist species of the type of habitat studied.

An increase in richness over the landscape does not simply translate into an

increase in its ecological value, as pointed out by several authors [41]. In our work, we set out to study the effects of the various fragmentation metrics on the abundance of a single species, not only because this is the first step towards building models with more elaborate response variables, but also because there is a monotonic relationship between single species abundance and the ecological value of the landscape. In an isolated system of single population dynamics, a landscape with a greater species abundance always has greater ecological value.

When it comes to purposes of conservation of species, our results suggest that highly fragmented landscapes may be detrimental to the number of species if the matrix quality is sufficiently poor, leading to eventual extinction at large values of κ, i.e. low matrix quality, especially at habitat amounts below 30%, which is very close to the percolation threshold of patches on the landscape, as proposed by Andrén (1994) [5]. Further investigation can be achieved with the model of reaction-diffusion equations presented here, adapting it to simulate several species through the addition of interspecific terms in the reaction. Although it is a straightforward generalization, simulating systems of several species raises mathematical complexities, such as multi-stability, dependence on initial conditions or periodic behaviours. But most importantly, the conclusions of such simulations should be inspected in the light of ecological scenarios of parameters rather than statistical analysis of increments of richness on synthetic data.

Chapter 5

Final considerations

Through the generation of synthetic data, we were able to test statistical models for the effects of habitat fragmentation under the assumption of minimal ecological mechanisms of growth and movement. Our statistical descriptions related geographical information about the spatial distribution of habitat in landscapes with the total abundance of a single species.

We extensively argued that fragmentation effects on the abundance of single species is possible in different directions and hence further characterization of the hostility (or quality) of matrix is necessary in order to determine both intensity and direction of these effects. Our results point towards further investigation of when and how fragmentation effects are positive or negative instead of the common attempt for a single generalization of empirical studies.

We highlighted the significance of insights that mathematical models can give to ecology. We believe that this simplified model can yet be a very useful tool to explore concepts and hypothesis of habitat fragmentation in single species and communities.

5.1 Perspectives

This model can be adapted to the study of different landscape aspects. For instance, one could include more classes of habitat within landscapes, simulating the variety of habitat quality commonly observed. Other aspects, as habitat edges, can also be modelled as an habitat class, and it could help understanding the ecological responses to edges and interfaces. These effects can also be modelled by an asymmetric patch-matrix movement in the interface due to patch preference, e.g. $\alpha \neq 1/2$ in Eq. (2.5), and it could be related to positive and negative edge effects observed in several empirical studies [13].

The model also permits to calculate the correlations between patch-level and landscape-level ecological responses, testing for an optimal scale to measure

fragmentation metrics in a circular buffer around the focal patch and different granularities of landscapes, given that there is an extensive literature on the effects of spatial scale to measure both fragmentation metrics and responses [41, 42, 49]. Patch-level responses are extremely important when addressing natural landscapes, given the heterogeneous patterns of fragmentation across natural landscapes.

Although considering in the model interacting species is very straightforward mathematically, it will add a new degree of complexity to the outcome of the model, requiring greater efforts on the quantification of results. The effects of the degree of fragmentation to the possibility of coexistence and biodiversity can be explored (TBP).

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