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A methodology to assess habitat fragmentation effects through regional indexes: illustration with forest biodiversity hotspots

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Graphical abstract

Highlights

- A methodology to derive worldwide regionalised fragmentation indexes is developed.
- It was applied to all forest ecoregions included in the biodiversity hotspots.
- The results highlighted significant intra- and inter-ecoregions differences.
- These indexes can be used for land use planning or macro-scale conservation planning.

Abstract

The fragmentation of natural environments is a critical issue involving major challenges for biodiversity conservation and ecosystem management. Large-scale information on areas sensitive to fragmentation is needed to improve the effectiveness of planning efforts. One promising metric combining the landscape spatial configuration with species characteristics is the metapopulation capacity λ , which can be used to rank different fragmented landscapes in terms of their capacity to support viable metapopulations. A methodology to globally derive a fragmentation metric based on metapopulation capacity, at appropriate and meaningful spatial scales for fragmentation mechanisms, was developed. To illustrate the applicability and interest of the methodology, worldwide regionalised fragmentation indexes, calculated with a dispersal distance of 1 km valid for a broad range of species, were provided for all forest ecoregions included in the *biodiversity hotspots*. Ecoregions were divided by a virtual grid and a statistical analysis of metapopulation capacity values calculated at the grid square scale was performed to obtain a Forest Fragmentation Potential *FFP* at three levels of spatial aggregation within the ecoregion (highly converted forest, entire forest, and the whole ecoregion). The results highlighted significant intra- and inter-ecoregions differences, showing great potential to extend

the use of these indexes to land use planning and areas prioritisation for both ecological protection and restoration. The influence of the different parameters used in the proposed approach is discussed as well as the limitations of the main assumptions. One important result is that the derived methodology can be easily adapted to a large number of species, scales, or regions to improve the coverage of fragmentation indexes.

Keywords

Landscape spatial configuration; Forest loss; Metapopulation capacity; Large-scale indexes; Biological conservation; Global maps

1. Introduction

In December 2016, the Conference of Parties for the Convention on Biological Diversity (COP13) gathered together 196 countries in Cancún with the objective of stopping the dramatic decline of terrestrial and marine biodiversity. WWF recently estimated that by 2020, at the current biodiversity loss rate, the world will have witnessed a two-thirds decline in global wildlife populations in only half a century (WWF, 2016a). And yet, of the twenty Aichi biodiversity targets (Convention on Biological Diversity, 2016), only four are partly reached or in the process of being reached, while for all others the situation still stagnates or even worse, for five of them, deteriorates (e.g. damages to coral reefs, pollution from excess nutrients, or most endangered species protection) (Secretariat of the Convention on Biological Diversity, 2014). Increasing international trade in our globalised economy accounts for a significant share of biodiversity threats (Chaudhary and Kastner, 2016; Lenzen et al., 2012; Moran and Kanemoto, 2017). In particular, consumers in developed countries cause threats to species through their

imported supplies from developing countries (Moran and Kanemoto, 2017). Similarly, numerous Life Cycle Assessment (LCA) studies showed that complex international value chains have environmental impacts, among others on biodiversity, all over the planet (de Baan et al., 2015; Hellweg and Mila i Canals, 2014). Land conversion from primary ecosystems to urban, industrial or agricultural land is a major biodiversity threat that has been studied for some years. The importance of subsequent environmental fragmentation, for which the situation is getting worse with respect to the corresponding Aichi biodiversity target (Convention on Biological Diversity, 2016), has been recognised more recently. However, to date most fragmentation studies have focused on the local scale whereas there are few analyses at regional scales or they are limited to the temperate zone or the tropics (Bregman et al., 2014). Except for a pioneering work that identified global fragmentation hotspots for mammalian carnivores (Crooks et al., 2011), global patterns of habitat fragmentation and connectivity have not yet been examined, even if long-term experiments indicated that fragmentation effects are considerable and clearly consistent across a diverse range of terrestrial systems on five continents (Haddad et al., 2015). A study conducted at the biogeographical scale also showed that incorporating fragmentation metrics into large-scale models may contribute for a better understanding of species distributions (Reino et al., 2013). With this in mind, global maps characterising the impacts of habitat fragmentation on species with relevant ecological indicators would be very useful for taking the appropriate decisions and actions for biodiversity conservation (GEO BON, 2015).

Fragmentation is commonly defined as a landscape-level process in which ‘a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original’ (Wilcove et al., 1986). Landscape structuration analysis is commonly conducted in parcels ranging in size from around 3 km² to 300 km²

(Fischer and Lindenmayer, 2007), and often set to 100 km² for different species in various studies (Atauri and de Lucio, 2001; Radford et al., 2005). Fragmentation typically leads to the reduction of landscape connectivity, which is defined as the degree to which the landscape facilitates or hinders organisms movements among habitat patches (Taylor et al., 1993). Management to maintain or restore connectivity is crucial to ensure the survival of many species and preserve biological diversity. Therefore, many authors proposed metrics to measure habitat connectivity at the landscape scale (Kindlmann and Burel, 2008; Ortega, 2010; Wang et al., 2014). Calabrese and Fagan (2004) proposed to distinguish between three main classes of connectivity metrics. First, the *structural connectivity* can be directly derived from landscape physical attributes (e.g. composition, shape or configuration metrics (Rutledge, 2003)). These types of indicators range from ‘simple’ landscape structure metrics (e.g. number of fragments) to more complex landscape indices (e.g. effective mesh size (Jaeger, 2000)), and dedicated software such as Fragstats (McGarigal, 1994) or, more recently, Conefor (Saura and Torne, 2009) have been developed to easily compute them on different spatial levels. Data has also been collected to quantify *structural* fragmentation globally (Haddad et al., 2015; Riitters et al., 2000). Second, the *potential connectivity* combines the landscape physical attributes, obtained from the structural connectivity analysis, with information on the focal species dispersal ability. Finally, the *actual connectivity* is based on observed or quantified (e.g. through species distribution models) movement pathways in the landscape. Structural connectivity is the easiest to collect, but it has a limited interest since it does not consider the species characteristics. The structural metrics ecological relevance (i.e. their relationship with the actual ecological processes taking place in the landscape) is often unproven and questionable (Kupfer, 2012). Conversely, actual connectivity gives very detailed information on the landscape but requires a large amount of

data, and consequently hinders its implementation at larger scales. Thus, potential connectivity metrics seem to be a sound compromise for providing reasonable estimates of functional connectivity, i.e. species behavioural responses to landscape patterns (Kindlmann and Burel, 2008), while being applicable at large-scale due to low data requirements.

One promising landscape potential connectivity metric at large-scale is the metapopulation capacity λ derived from metapopulation theory (Hanski and Ovaskainen, 2000). Hanski and Ovaskainen defined the metapopulation as a group of spatially separated populations of the same species interconnected by dispersal. In particular, the metapopulation capacity λ measures how a given spatial configuration of a set of fragments contributes to the long-term persistence of a particular species structured as metapopulation. This indicator has been widely used to estimate the fragmentation effects in various landscapes, e.g. agricultural landscapes (Hietala-Koivu et al., 2004), forest landscapes (Pardini et al., 2010; Schnell et al., 2013a), or fluvial landscapes (Bertuzzo et al., 2015), and it has also been tested and explored further on simulated landscapes (Grilli et al., 2015; Rybicki and Hanski, 2013). Although the metapopulation capacity λ may be a promising indicator of landscape fragmentation, for now its use is limited to specific local landscapes. The aim of this paper is to develop an easily appropriable and parsimonious methodology to derive worldwide regionalised fragmentation indexes based on λ and to demonstrate the applicability and interest of this methodology with a dispersal distance of 1 km fitting a wide variety of species on all forest ecoregions in the *biodiversity hotspots* (Myers et al., 2000; Russell A. Mittermeier et al., 2004) as they are the richest and the most threatened plant and animal life reservoirs on Earth (Conservation International, 2016). This preliminary assessment will provide a global overview of the current abilities of birds or mammals with dispersal distances around 1 km to persist in the hotspots, which can be very useful in

environmental assessment studies such as ones conducted in LCA or in footprint analyses. The innovative methodology itself also opens up vast prospects for biological conservation: with specific parameters adapted to a particular species in a specific region, its use could be extended to land use planning and areas prioritisation for both ecological protection and restoration.

2. Materials and methods

We used spatially explicit metapopulation models (Hanski, 1998; Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001) to describe habitat fragmentation at regional scales (e.g. ecoregion scale), since the metapopulation capacity λ can conveniently be used to rank different fragmented landscapes in terms of their capacity to support viable metapopulations. This section will present 1) the conventional metapopulation capacity calculation at the landscape scale and then 2) a methodology to extend it to large regions.

2.1. Metapopulation capacity of a species in a single landscape

Formally, in metapopulation theory, metapopulation capacity λ is given by:

$$\text{Leading eigenvalue } \lambda \text{ of matrix } \mathbf{M} \text{ with elements } m_{ij} = \begin{cases} A_i^x A_j^y f(d_{ij}), & i \neq j \\ 0, & i = j \end{cases} \quad (1)$$

Where A_i and A_j are respectively the areas of fragments i and j , d_{ij} is the Euclidian distance between the centroids of fragments i and j , and $f(d_{ij})$ is a dispersal function describing how the species arrival rate drops off with the distance d_{ij} between fragments. The exponents x and y are scaling factors for the fragment area that depend on the extinction rate, the immigration rate and the emigration rate. The function $f(d_{ij})$ commonly presented is a negative exponential $e^{-\alpha d_{ij}}$, in which α is the inverse of the species average dispersal distance. We adopted the following exponential dispersal kernel with a cut-off at 0.01 (equation 2) proposed by Hanski et al. (2013):

$$f(d_{ij}) = \max\{e^{-\alpha d_{ij}}, 0.01\} \quad (2)$$

Nevertheless, in original metapopulation models, colonisation is defined as a between-patch movement and there is no colonisation from a patch to itself. As a consequence, the original metapopulation capacity λ of a single patch—no matter how large it is, and even if the whole landscape consists of one patch—is zero, because it received no colonisation from surrounding patches. To overcome the non-intuitive behaviour of this metric for systems of a few large patches, Schnell et al. (2013b) recently adapted the original metapopulation model by adding a self-colonisation component that gives large patches the potential to harbour small numbers of survivors following an extinction event which will be able to recolonise the rest of the patch. In the model with self-colonisation, $m_{ij} = A_i^x A_j^y$ when $i = j$. Consequently, with the self-colonisation metapopulation capacity λ_{self} , a single large patch has the highest metapopulation capacity and subsequent fragmentation decreases the metric. Like λ , λ_{self} is a measure that combines overall area and fragmentation, and provides a consistent relative ranking of landscapes.

2.2. Computing statistics on λ_{self} calculated at the grid square scale for a large region

For the environmental assessment of human activities, baseline indicators on regional habitat fragmentation would be useful for decision-making along globalised supply chains (i.e. along product or service life cycles). However, the metapopulation capacity should be quantified at a scale that is relevant for the focal species. According to Olson et al. (2001), the ecoregion average area is about 150,000 km² (median $\approx$ 60,000 km²) while the biodiversity hotspots have a mean surface area around 800,000 km² (median $\approx$ 300,000 km²). Given that the sizes of these biogeographic units are both much larger than the model species dispersal abilities, it would be ecologically meaningless to directly calculate the metapopulation capacity at such spatial scales.

Thus, to compute λ_{self} for larger areas, we divided the entire region of interest by a virtual grid and calculated $\lambda_{self,GS}$ for selected Grid Squares (GS) (see Figure A1 in Appendix A). The landscape structure was characterised by a nonhabitat *matrix* surrounding native habitat fragments. Using Q-GIS (QGIS Development Team, 2017), the habitat fragment centroids were identified, and the data necessary to calculate $\lambda_{self,GS}$ were extracted, i.e. each fragment size A_i , and its centroid coordinates X_i , Y_i . The distances d_{ij} between the fragment centroids within each grid square were calculated, then, by introducing the dispersal distances of the modelled species, $\lambda_{self,GS}$ was calculated according to equation 1 (see Appendix A, Section 1-E for programming details).

2.3. Deriving fragmentation indexes for large regions based on $\lambda_{self,GS}$ statistics

Statistical analysis of $\lambda_{self,GS}$ values calculated at the grid square scale can be used to obtain fragmentation indexes for a whole region.

Several studies support the hypothesis that fragmentation effects follow a threshold function related to the remaining available habitat. When habitat area is still large enough, fragmentation can have a positive impact, i.e. by increasing the local species richness, but which will be hidden by the superior, negative habitat loss effects. When the habitat area falls below a critical threshold, generally around 20-30% (Andren, 1994; Flather and Bevers, 2002; Hanski, 2015; Pardini et al., 2010; Schneider, 2001), the fragmentation effects become negative, affecting species survival, and should not be ignored. Consequently, $\lambda_{self,GS}$ were exclusively derived for grid squares with less than 30% of their original vegetation (defined as *Conditions of λ_{self} validity* in [Figure 1](#)~~Figure 1~~). Original or native vegetation can refer to various ecosystems (among others, grasslands, savannas, forests, or deserts). In this study, only primary forest ecosystems were considered and $\lambda_{self,GS}$ was not calculated for grid squares with no primary forest at all.

Based on $\lambda_{self,GS}$ values of all grid squares in which forest cover ranges from $>0\%$ to $\leq 30\%$ —thereafter referred to as ‘highly converted forest’—, we can determine a median value $\lambda_{self,j}$ of the non-normally distributed $\lambda_{self,GS}$ (Figure A2 in Appendix A), that stands for the metapopulation capacity of the whole large region j most converted forest areas (grey box in [Figure 1](#)).

Figure 1: Methodology for calculating the fragmentation indexes (*Forest Fragmentation Potential FFP*) of a large region at three levels of spatial aggregation (highly converted forest, forest and the entire region). P: Percentile. NC: Not calculated.

Once $\lambda_{self,j}$ has been computed for each large region j (e.g. ecoregions), the median values of all large regions are ranked from the 2.5th percentile (P2.5) to the 97.5th percentile (P97.5).

Subsequent winsorising reduces the effect of possible outliers by limiting extreme values in the data via setting outliers to a data specified percentile. Here, a 95% winsorising was applied, meaning that all data below the 2.5th percentile are set equal to the 2.5th percentile ($=\lambda_{self,min}$) and all data above the 97.5th percentile are set equal to the 97.5th percentile ($=\lambda_{self,max}$). A 95% winsorising was found to deal adequately with extreme values without being too exclusive on the dataset. Normalisation from 0 (low fragmentation stress) to 1 (high fragmentation stress) provides a commensurable and dimensionless index, i.e. the Forest Fragmentation Potential of highly converted forests $FFP_{Forest \leq 30\%,j}$ of a large region j according to equation 3. In this way, the 5% extreme values of the global dataset, i.e. the least fragmented regions ($\lambda_{self} \geq P97.5$) and the most fragmented regions ($\lambda_{self} \leq P2.5$), have a Forest Fragmentation Potential set to 0 and 1, respectively. In between, the fragmented regions are classified according to their fragmentation degree.

$FFP_{Forest \leq 30\%,j}$ indicates the fragmentation ‘state’ of the most critical forest areas within region j . The more region j is fragmented, the smaller is $\lambda_{self,j}$ and the higher is $FFP_{Forest \leq 30\%,j}$:

$$FFP_{Forest \leq 30\%,j} = \frac{(\lambda_{self,max} - \lambda_{self,j})}{(\lambda_{self,max} - \lambda_{self,min})} \quad (3)$$

To characterise the Forest Fragmentation Potential of the whole region $FFP_{Forest,j}$, we weight $FFP_{Forest \leq 30\%,j}$ by the proportion between the highly converted forest grid squares and the total number of forest grid squares in region j $FS_{\leq 30\%}^{FOREST,j}$:

$$FFP_{Forest,j} = FFP_{Forest \leq 30\%,j} \times FS_{\leq 30\%}^{FOREST,j} \quad (4)$$

$$\text{With } FS_{\leq 30\%}^{FOREST,j} = \frac{\sum \text{GS, with } 0\% < \text{forest cover} \leq 30\%}{\sum \text{GS, with } 0\% < \text{forest cover} \leq 100\%}$$

Finally, to determine the whole region fragmentation state, we use the regional forest area proportion, defined as the ratio of forest grid squares and total number of grid squares (i.e.

including forest-free grid squares) in the region ($FS_{\frac{\text{FOREST}}{\text{TOTAL}}}$ in equation 5). The Forest Fragmentation Potential $FFP_{All,j}$ expresses the forest fragmentation potential for the whole large region j (e.g. an ecoregion):

$$FFP_{All,j} = FFP_{Forest,j} \times FS_{\frac{\text{FOREST}}{\text{TOTAL}}}$$
 (5)

$$\text{With } FS_{\frac{\text{FOREST}}{\text{TOTAL}}} = \frac{\sum \text{GS, with } 0\% < \text{forest cover} \leq 100\%}{\sum \text{GS}}$$

2.4. Implementing the methodology on forest ecoregions included in the biodiversity hotspots

For a global implementation, we first focus our assessment on the biodiversity hotspots. To qualify as a biodiversity hotspot, a region must meet two criteria, i.e. 1) holding high numbers of endemic vascular plants, and 2) having 30% or less of its original vegetation (Conservation International, 2016), thus corresponding to the ‘fragmentation threshold’ mentioned above, below which considering fragmentation is relevant. Furthermore, Sloan et al. (2014) recently provided updated estimates of natural, intact vegetation within these hotspots that show that their state could be even more critical than previously described. We considered all ecoregions included in the biodiversity hotspots with a focus on forest major habitat types (see Appendix A, Section 1–B for more details). Area loss in forests is rarely simply the removal of contiguous areas and these habitats are particularly experiencing fragmentation (Whitmore and Sayer, 1992), mainly because of industrial timber extraction, agricultural expansion, fire, and resource extraction (Potapov et al., 2017). Due to fragmentation, the number of intact forest landscapes (larger than 500 km²) is decreasing drastically, around 7% in 13 years, particularly in tropical regions (Potapov et al., 2017). Thus, forests are under pressure like never before, while they host 90% of terrestrial species (WWF, 2016b).

We applied the methodology developed ([Figure 1Figure 1](#)) to all biodiversity hotspots that contain forest ecoregions (i.e. 34 forest hotspots: six in Africa, fourteen in Asia-Pacific, four in Europe and Central Asia, five in North and Central America, and five in South America). 259 ecoregions met the conditions for $\lambda_{self,j}$ calculation (see *Conditions of λ_{self} validity* in [Figure 1Figure 1](#)), and FFP_j were provided for a total of 283 ecoregions, because fragmentation indexes of the 24 ecoregions for which all whole grid squares had a forest cover higher than 30% were set to 0 (see right side of [Figure 1Figure 1](#)). Details on spatial processing can be found in Appendix A, Section 1–D.

2.5. Input data for model parameters

Two kinds of data are required to implement the developed methodology, i.e. 1) species characteristics (dispersal ability and scaling factors), and 2) landscape inputs (original habitat choice, map resolution, and grid size for spatial analysis). For each of them, data constraints and availability are discussed to select the most appropriate data for the λ_{self} global calculation (Table A1 in Appendix A).

Species data are essential for the metapopulation capacity model. Provided that ‘forest’ is its habitat, a species can be heavily or slightly affected depending on its ability to move ($1/\alpha$, in connection with d_{ij}), and on its immigration and extinction abilities (x and y , related to A_i). Various ‘dispersal distances’ are reported in literature, e.g. the median, mean and maximum dispersal distances, and the migratory distance. The differences between these variables are hard to capture because their calculation varies depending on the author. Furthermore, there is a large variability associated with species dispersal distances, depending on their size or migratory habits. Based on a literature review of available species dispersal distances (Sutherland et al., 2000), we arbitrarily considered a 1 km dispersal distance, which can apply to some birds and

mammals, as a first example of the methodology application. Regarding scaling factors x and y , Hanski et al. (2013) give a x realistic value for birds and mammals (1.5), while Schnell et al. (2013b) propose another value valid for many taxa (0.5). Both studies considered a y value of 1. We used the values provided by Schnell et al. (2013b) because they offer a broader choice in terms of applications to different taxa.

The fragmentation assessment strongly depends on the land cover of interest definition (Riitters et al., 2000). In this work, we used Globcover 2009 maps (Bontemps et al., 2011), produced by the European Space Agency, which count 22 land cover classes. Among them, several classes can be included in the forest definition, and considering only class 50 *Closed* (>40%) *broadleaved deciduous forest* (>5m), both classes 50 and 40 *Closed to open* (>15%) *broadleaved evergreen or semi-deciduous forest* (>5m), or all eight potential forest classes combined, can have a large influence on the results, underestimating or overestimating the real forest cover. Furthermore, reports usually describe the remaining original habitat area in percentage ‘of its original extent’ (CEPF, 2016; Di Bitetti et al., 2003), but all the ecoregion was not necessarily covered with this original habitat (other land covers, water bodies, mountains, etc.). To simplify our methodology, we considered all Globcover 2009 forest classes.

Map resolution is also a crucial parameter, since the notion of ‘fragment’ strongly depends on the scale considered. Many metrics indicated lower fragmentation at coarser spatial resolutions (Saura, 2004), and a recent study showed that metapopulation capacity is sensitive to the spatial scale at which the habitat units were defined (Blazquez-Cabrera, 2014). Maps with smaller resolutions identify more non-forest area where forest cover is dominant but not exclusive. Hanski et al. (2013) used a map resolution of 30 m, but they used a bird species dispersal distance much smaller (300 m) than the median value found in literature, i.e. 4 km for birds

(Sutherland et al., 2000). A transposition based on ecological parameters would lead to a scale-up of a factor ten for map resolution (400 m). Thus, we took Globcover 2009 (300 m resolution) for land cover data.

Likewise, fragmentation can turn out greater when larger grid sizes are used (Riitters et al., 2000). Consequently, to perform a meaningful metapopulation capacity calculation, it is essential to define spatial scale(s) at which metapopulation processes predominantly take place. Olson et al. (2001) examined a moth metapopulation with a measured dispersal distance of 100 m at four levels of spatial analysis and concluded that metapopulation processes were important at the regional and sub-regional scales (i.e. $\approx 35 \text{ km}^2$ and $\approx 10 \text{ km}^2$, with 100 m and 50 m resolutions respectively). Consequently, for dispersal distances ranging from 500 m to 5 km, spatial scales between 50 and 2000 km^2 would be consistent, with associated resolutions ranging from 250 m to 5 km. Following the same logic as for map resolution, we could also have scaled-up the grid size for λ_{self} calculations based on Hanski et al. (2013), but we found 100 km^2 more adapted to the range of ecoregion sizes. 1000 km^2 grid squares were too large to adequately reflect some small ecoregions, e.g. for the *Montane Fynbos And Renosterveld* ecoregion (AT1203), only three grid squares were larger than 950 km^2 , representing only 6% of the whole ecoregion area. Thus, a 100 km^2 -grid was applied to each hotspot, and grid squares larger than 95 km^2 (5% margin) were selected for each ecoregion. Consequently, all ecoregions smaller than the grid square size (100 km^2) were excluded from the outset, representing less than 0. 2% in surface of all forest ecoregions belonging to the biodiversity hotspots.

3. Results

3.1. Spatial representation of the three FFPs

The FFP s of all 30 ecoregions included in the Indo-Burma hotspot are spatially represented for each 100-km² grid square included in the hotspot ([Figure 2Figure 4](#)). $FFP_{Forest \leq 30\%,j}$ is a median value of the most critical forest areas fragmentation ‘state’ within the ecoregion j , thus only grid squares in which forest cover is smaller than 30% are concerned (upper-map in [Figure 2Figure 4](#)). $FFP_{Forest \leq 30\%}$ can be used to assess the potential impact on biodiversity of a current or future activity using land in a highly converted forest area. As FFP_{Forest} weights the previous index by the total forest cover in the ecoregion, the index value is affected to all forest grid squares (middle-map in [Figure 2Figure 4](#)). FFP_{Forest} can be used to compare activities for which land use surely occurs in a forest area, with no additional information on the forest cover. Lastly, FFP_{All} applies to all grid squares in the ecoregion (lower-map in [Figure 2Figure 4](#)) and can be used to rank land use impacts in different ecoregions when the exact locations of activities in the ecoregions are unknown. The more spatially aggregated the fragmentation indexes (from $FFP_{Forest \leq 30\%}$, then FFP_{Forest} , to finally FFP_{All}), the more uncertain they are.

More explanations on the different indexes are given with the example of the Indo-Burman ecoregions A, B and C ([Figure 2Figure 4](#)). All three ecoregions have a high $FFP_{Forest \leq 30\%}$ (respectively 0.92, 0.82 and 0.99), which means that their most converted forest zones are highly fragmented and have a strong negative impact on species (compared to other ecoregions worldwide). Overall forest, however, is less damaged in ecoregion B than in ecoregions A or C, i.e. grid squares with less than 30% of forest are scarcer in ecoregion B, so $FFP_{Forest,B}$ (0.10) is much lower than $FFP_{Forest,A}$ (0.56) or $FFP_{Forest,C}$ (0.86). However, almost all 100 km² grid squares contain forest in both ecoregions A and B whereas ecoregion C contains many forest-free grid squares, so $FFP_{All,A}$ (0.54) and $FFP_{All,B}$ (0.10) are close to $FFP_{Forest,A}$ and $FFP_{Forest,B}$ whereas $FFP_{All,C}$ (0.18) decreases considerably compared to $FFP_{Forest,C}$.

Figure 2: Fragmentation indexes for forest ecoregions included in the *Indo-Burma* biodiversity hotspot calculated for a species dispersal distance of 1 km; arrow A points to *Meghalaya Subtropical Forests* (ecoregion IM0126), arrow B points to *Chin Hills-Arakan Yoma Montane Forests* (ecoregion IM0109), and arrow C points to *Irrawaddy Dry Forests* (ecoregion IM0205)

3.2. Global maps of FFPs

The fragmentation indexes were calculated for each forest ecoregion included in the biodiversity hotspots for an illustrative species dispersal distance of 1 km. Global map of FFP_{All} is presented in [Figure 3](#), and equivalent maps for $FFP_{Forest \leq 30\%}$ and FFP_{Forest} are displayed in Figure A3 and Figure A4 in Appendix A. All raw data for $FFP_{Forest < 30\%}$, FFP_{Forest} and FFP_{All} can be found in Appendix B (separate Excel file).

Figure 3: Forest Fragmentation Potential FFP_{All} for all forest ecoregions included in the biodiversity hotspots (coloured areas) calculated for a species dispersal distance of 1 km

The most converted forests within the ecoregions (i.e. $0\% < \text{forest cover} \leq 30\%$) globally show a high fragmentation potential (Figure A3 in Appendix A). Only 42 out of the 259 ecoregions for which λ_{self} was calculated have a fragmentation potential $FFP_{Forest \leq 30\%}$ smaller than 0.6, and 57 ecoregions (mainly in the *Paelearctic* and *Indomalayan* realms) have it higher than 0.95. However, $FFP_{Forest \leq 30\%}$ reflects the fragmentation potential of already altered forest areas, and does not reflect the forest ‘state’ of the whole ecoregion.

FFP_{Forest} i.e. $FFP_{Forest \leq 30\%}$ weighted by the proportion of highly converted forest zones compared to all forest zones, provides more distributed results globally (Figure A4 in Appendix A). Only 22 ecoregions, mainly in Indo-Burma, Mediterranean Basin and Irano-Anatolian hotspots, present FFP_{Forest} higher than 0.90. In addition, there are strong differences between $FFP_{Forest \leq 30\%}$ and FFP_{Forest} results (respective median values of 0.86 and 0.27), which indicate that fragmentation is most frequently a process confined to relatively specific geographical areas. For instance, some ecoregions have highly fragmented forests (high $FFP_{Forest \leq 30\%}$), but only over

a small part of their total forest area (low FFP_{Forest}). The spatial aggregation at the ecoregion scale tends to smooth the results.

FFP_{All} , weighted in proportion to ecoregion forest areas, has values very similar to FFP_{Forest} (global median of 0.23). This is because there are few landscapes (100 km² grid squares) with no forest at all (i.e. the forest share $FS_{\frac{FOREST}{TOTAL}}$ often approaches 1), which is expected for ecoregions with forest as major habitat types. Nevertheless, for some ecoregions, e.g. for the four North African ecoregions included in the *Mediterranean Basin* hotspot, FFP_{Forest} can be high and FFP_{All} much lower, due to their small forest cover. Conversely, e.g. in Indonesia or South America, both FFP_{Forest} and FFP_{All} can be high because of some ecoregions large forest share. Only three ecoregions have FFP_{All} higher than 0.9, and they all are in the *Neotropical* realm (ecoregions NT0233 *Veracruz Dry Forests*, NT0102 *Atlantic Coast Restingas* and NT0151 *Pernambuco Coastal Forests*).

4. Discussion

An easily appropriable and performing methodology to derive worldwide regionalised λ -based fragmentation indexes at meaningful scales for fragmentation mechanisms was built, and applied to an illustrative, arbitrary example (by setting the species dispersal distance to 1 km, and using scaling factors adapted to birds or mammals). The objective was twofold: (1) to test the feasibility of the method at a worldwide scale, and (2) to evaluate the resulting indexes' ability to provide valuable information on fragmentation stresses. The methodology was successfully applied in about 300 ecoregions all over the world, and the resulting indexes clearly confirmed significant intra- and inter-ecoregions differences regarding landscapes' fragmentation stresses. These results open up prospects for promising applications of the methodology to real ecological studies. However, the proposed methodology still faces some methodological and practical limitations and still has room for improvement.

4.1. Metapopulation model limitations

The interest of metapopulation theory to explain variations in species occurrence patterns in highly fragmented landscapes has been recognised. However, metapopulation theory implies that the populations exist in patchy distributions. When there is no evidence for metapopulation dynamics in a given species or region, this approach might not be valid. As a great range of dispersal models are available in the literature, the more adapted and realistic dispersal functions $f(d_{ij})$ should be incorporated in spatial models when possible (Travis and French, 2000). In the proposed methodology, due to the metapopulation model flexibility, other more complex dispersal functions could easily replace the proposed one if needed. Furthermore, because

species dispersal still needs to be better understood and assessed, new ecological developments and data could also be easily incorporated in the model as soon as they become available.

Modelling metapopulation dynamics is a very useful tool for conservation ecology. However, metapopulation models have historically treated a landscape as a collection of habitat patches — in our case, forest—separated by a homogenous, permeable but unsuitable habitat usually called *matrix*—in our case, non-forest—. In these models, movement between patches depends only on the distance between patches and the inherent species dispersal ability, and the matrix structure and quality effects on movement through the landscape are neglected. Yet, even if theoretical and empirical evidence show that matrix quality can be extremely important in determining metapopulation dynamics (Vandermeer and Carvajal, 2001), these factors are rarely incorporated into metapopulation models. In particular, linear infrastructure such as road networks can considerably hinder species movements (often referred to as the ‘barrier effect’ in ecology (Forman and Alexander, 1998)) and have a strong negative impact on species (Loro et al., 2015). Moreover, this barrier effect varies among species, which are not similarly affected by a given barrier. Gebauer et al. (2013) investigated the importance of matrix type for metapopulation modelling and found that it had as much or sometimes more influence than patch sizes or distances between patches on metapopulation parameters. The use of mathematical tools enabled by the matrix-modelling framework, such as sensitivity and elasticity analyses (Shima et al., 2010), or the incorporation of a matrix resistance parameter, which is expected to vary among species (Ricketts, 2001), could definitively improve metapopulation modelling. If matrix quality was to be included in the metapopulation model, complementary road maps could be used in addition to Globcover 2009 maps to capture the barrier effects induced by linear infrastructure.

Finally, the metapopulation capacity assesses species persistence in fragmented landscapes, which is a limited aspect of all possible ecological attributes and levels of biodiversity organisation, which encompasses not only species composition but also ecosystem structure and functions.

4.2. Data availability and uncertainty

There is inherent uncertainty in data (e.g. land cover maps, species dispersal distances), on choices associated with data treatment, and on the metapopulation model itself, i.e. to what extent does it reflect real species behaviour. The results should hence be interpreted in light of this information (Langford et al., 2006). Globcover 2009 maps are among the most detailed, reliable and up-to-date global land cover maps. Their overall accuracy weighted by the class area reaches 67.5%. The Globcover 2009 resolution (300 m) is consistent with the spatial scale considered (i.e. global statistics on 100 km²-landscapes), and execution times for the associated spatial processing are acceptable. Regarding species data, the selected dispersal distances were chosen to be of the same order of magnitude than estimates derived from empirical data from a global literature review (Sutherland et al., 2000). The uncertainty associated with these estimates is very closely linked to the natural data variability. A way to overcome this shortcoming would be to generate more results to cover a more complete range of species dispersal distances. As more biodiversity monitoring data will become available, these dispersal distances estimates should be updated and results accuracy will be improved. Moreover, the indexes could be combined with data on specific species effectively inhabiting each ecoregion to enhance the results relevance. Another interesting development would be to weight the indexes by the threatened status and/or the level of species endemism, e.g. percent endemism by taxonomic group in each hotspot (CEPF, 2016).

The λ_{self} sensitivity to several crucial parameters related to 1) land cover data (original habitat and maps resolution), 2) grid size, and 3) species data (dispersal distance and scaling factor x) was assessed and the results can be found in Appendix A, Section 3–A. Other data or methodological choices likely to affect the results were also discussed in the same section. However, even if some parameters may have a great influence on λ_{self} , no change in these will affect their *ranking* (i.e. for ecoregions ranking). The λ_{self} final *distribution* and subsequent *FFP* indexes derived from λ_{self} , might be affected though, given that the λ_{self} dependency on the input parameters and choices is not necessarily linear.

Regarding the fragmentation index calculation based on λ_{self} statistics, the $\lambda_{self,GS}$ values aggregation for large regions (e.g. ecoregions), by means of the median, is another important source of uncertainty, due to the intra-ecoregion spatial variability. As an example, the $\lambda_{self,GS}$ spatial variability of the larger forest ecoregion included in the biodiversity hotspots, i.e. *Alto Paraná Atlantic Forest* (ecoregion NT0150), is illustrated in Figure A5 in Appendix A. The results show that, rather than being distributed evenly throughout the ecoregion, fragmentation can be very critical in some specific places of the ecoregion. Similarly to other stress indexes (e.g. water stress), a global or regional fragmentation stress can strongly differ from a local stress, and too aggregated stress values will be unrepresentative of the local reality.

Likewise, the definition and spatial resolution of Forest Shares *FS* used for *FFP* calculation may influence the results and is discussed in Appendix A, Section 3–C.

4.3. Applicability

The fragmentation indexes can be used directly to rank all highly fragmented forest ecoregions included in the biodiversity hotspots. As they are based on metapopulation capacity, which is already a relative measure, and given their strong sensitivity to the input parameters, the

fragmentation indexes should not be taken as absolute values and should be used for comparative purposes only. Assuming that the species dispersal ability is known and similar in magnitude to the considered dispersal distance, conclusions can be drawn for this particular species. However, for now, they are limited to a specific range of species dispersal distances, based on animal dispersal abilities statistics. Plants should also be considered, especially as metapopulation concept has been largely applied to plants through seed dispersal (Verheyen et al., 2004).

To overcome this problem, the proposed grid procedure and methodology for deriving metapopulation capacity statistics at regional scales was designed to be easily used and applied to other large datasets. Our analysis was restricted to biodiversity hotspots as defined by Myers et al. (2000), but other prioritisation approaches exist for global biodiversity conservation, and other templates may be considered (Brooks et al., 2006; Moran and Kanemoto, 2017). We also focused the scope of application on the ecoregions whose major habitat type was forest (i.e. approximately 70% in surface of all ecoregions belonging to the biodiversity hotspots), but other major habitat types, e.g. grasslands, could easily be incorporated. Conversely, the proposed methodology could also be applied to specific ecoregions or sub-ecoregions, with a grid size and a map resolution adapted to a particular species. To widen the range of model applications while ensuring reproducibility, and to ease new fragmentation indexes calculations, the matrix calculation program is available upon request.

4.4. Conclusions and perspectives

The global forest fragmentation is a critical issue facing major challenges for the biodiversity conservation and ecosystems management, particularly in tropical environments (Bregman et al., 2014), and especially since these effects may be worsened by other global changes caused by human activity, e.g. climate change (Haddad et al., 2015). Macro-scale conservation planning

gives a means of coping with the challenge arising from the environmental impacts of extensive land use changes for urban or agricultural activities (Olsoy et al., 2016). To this end, global information on areas sensitive to fragmentation is needed to improve the effectiveness of planning efforts.

Thus, an innovative methodology for modelling the fragmentation potential of large regions was proposed. The landscape spatial configuration is combined with a metapopulation model to obtain an ecologically relevant landscape fragmentation metric to compare any fragmented landscapes, producing an efficient tool for land management. The modelling approach applied in this work was developed to fit most species, provided that some adaptations are made to deal with species specificities. Indeed, the flexibility of the methodology allows the spatial parameters, e.g. the grid size and the map resolution, and the species parameters, e.g. the dispersal distance and the dispersal function of the metapopulation model, to be easily adapted to a specific species.

Secondly, as an example, we provide a first set of fragmentation indexes for ranking all forest ecoregions ($> 100 \text{ km}^2$) belonging to the biodiversity hotspots. These global maps are relevant to the subset of species corresponding to the types of habitat and to the dispersal capacities considered, and provide first-hand information on the ability of these species, i.e. birds or mammals with a dispersal distance of 1 km, to persist in highly fragmented habitats. These indexes can help decision makers, from producers, scientists, conservationists, to governments, to better target their actions. They can be used as a tool for land planners or industrial companies, for comparing different options regarding their activities locations at the ecoregion scale. Conversely, they enable focusing on areas where offset measures would have the most impact (Dalang and Hersperger, 2012). Finally, fragmentation metrics at large-scale can be used to

improve predictive modelling of range shifts associated with land use (Reino et al., 2013). More particularly, they could contribute to better assess the environmental impacts of a product using land at different places around the globe along its life cycle. To date, several indicators are available in LCA to quantify a certain number of land use impacts (e.g. the impact of decreasing their habitat quantity on species), but, until now, habitat fragmentation impacts are poorly considered. In this perspective, the fragmentation indicators should be calculated for each taxon usually considered for land use impacts in LCA, i.e. birds, mammals, reptiles, amphibians and vascular plants, using median values of species or seed dispersal distances and scaling factors for which estimates are available in the literature (see for example Kharouba et al. (2012); Sutherland et al. (2000) and Verheyen et al. (2004)). They should also be extended to other habitat types (e.g. grasslands, savannas, shrublands, tundra, mangroves and deserts). In addition, as they stand, the fragmentation indexes are stand-alone indicators which are not directly linked to a land use intervention. Incorporating them into analytical environmental assessment methods such as LCA will need further development.

Appendices

Appendix A: Additional methods and results (PDF)

Appendix B: Metapopulation capacities λ_{self} , forest shares FS , and FFP indexes for forest ecoregions included in the biodiversity hotspots for a 1 km species dispersal distance (XLSX)

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