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

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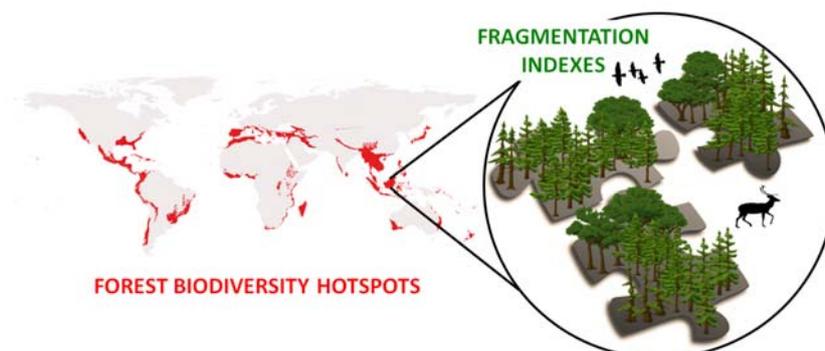
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11 **Graphical abstract**



13

14 **Highlights**

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

19 **Abstract**

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

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

40 **Keywords**

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

43

44 **1. Introduction**

45 In December 2016, the Conference of Parties for the Convention on Biological Diversity
46 (COP13) gathered together 196 countries in Cancún with the objective of stopping the dramatic
47 decline of terrestrial and marine biodiversity. WWF recently estimated that by 2020, at the
48 current biodiversity loss rate, the world will have witnessed a two-thirds decline in global
49 wildlife populations in only half a century (WWF, 2016a). And yet, of the twenty Aichi
50 biodiversity targets (Convention on Biological Diversity, 2016), only four are partly reached or
51 in the process of being reached, while for all others the situation still stagnates or even worse, for
52 five of them, deteriorates (e.g. damages to coral reefs, pollution from excess nutrients, or most
53 endangered species protection) (Secretariat of the Convention on Biological Diversity, 2014).
54 Increasing international trade in our globalised economy accounts for a significant share of
55 biodiversity threats (Chaudhary and Kastner, 2016; Lenzen et al., 2012; Moran and Kanemoto,
56 2017). In particular, consumers in developed countries cause threats to species through their

57 imported supplies from developing countries (Moran and Kanemoto, 2017). Similarly, numerous
58 Life Cycle Assessment (LCA) studies showed that complex international value chains have
59 environmental impacts, among others on biodiversity, all over the planet (de Baan et al., 2015;
60 Hellweg and Mila i Canals, 2014). Land conversion from primary ecosystems to urban, industrial
61 or agricultural land is a major biodiversity threat that has been studied for some years. The
62 importance of subsequent environmental fragmentation, for which the situation is getting worse
63 with respect to the corresponding Aichi biodiversity target (Convention on Biological Diversity,
64 2016), has been recognised more recently. However, to date most fragmentation studies have
65 focused on the local scale whereas there are few analyses at regional scales or they are limited to
66 the temperate zone or the tropics (Bregman et al., 2014). Except for a pioneering work that
67 identified global fragmentation hotspots for mammalian carnivores (Crooks et al., 2011), global
68 patterns of habitat fragmentation and connectivity have not yet been examined, even if long-term
69 experiments indicated that fragmentation effects are considerable and clearly consistent across a
70 diverse range of terrestrial systems on five continents (Haddad et al., 2015). A study conducted
71 at the biogeographical scale also showed that incorporating fragmentation metrics into large-
72 scale models may contribute for a better understanding of species distributions (Reino et al.,
73 2013). With this in mind, global maps characterising the impacts of habitat fragmentation on
74 species with relevant ecological indicators would be very useful for taking the appropriate
75 decisions and actions for biodiversity conservation (GEO BON, 2015).

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

80 (Fischer and Lindenmayer, 2007), and often set to 100 km² for different species in various
81 studies (Atauri and de Lucio, 2001; Radford et al., 2005). Fragmentation typically leads to the
82 reduction of landscape connectivity, which is defined as the degree to which the landscape
83 facilitates or hinders organisms movements among habitat patches (Taylor et al., 1993).
84 Management to maintain or restore connectivity is crucial to ensure the survival of many species
85 and preserve biological diversity. Therefore, many authors proposed metrics to measure habitat
86 connectivity at the landscape scale (Kindlmann and Burel, 2008; Ortega, 2010; Wang et al.,
87 2014). Calabrese and Fagan (2004) proposed to distinguish between three main classes of
88 connectivity metrics. First, the *structural connectivity* can be directly derived from landscape
89 physical attributes (e.g. composition, shape or configuration metrics (Rutledge, 2003)). These
90 types of indicators range from ‘simple’ landscape structure metrics (e.g. number of fragments) to
91 more complex landscape indices (e.g. effective mesh size (Jaeger, 2000)), and dedicated software
92 such as Fragstats (McGarigal, 1994) or, more recently, Conefor (Saura and Torne, 2009) have
93 been developed to easily compute them on different spatial levels. Data has also been collected
94 to quantify *structural* fragmentation globally (Haddad et al., 2015; Riitters et al., 2000). Second,
95 the *potential connectivity* combines the landscape physical attributes, obtained from the
96 structural connectivity analysis, with information on the focal species dispersal ability. Finally,
97 the *actual connectivity* is based on observed or quantified (e.g. through species distribution
98 models) movement pathways in the landscape. Structural connectivity is the easiest to collect,
99 but it has a limited interest since it does not consider the species characteristics. The structural
100 metrics ecological relevance (i.e. their relationship with the actual ecological processes taking
101 place in the landscape) is often unproven and questionable (Kupfer, 2012). Conversely, actual
102 connectivity gives very detailed information on the landscape but requires a large amount of

103 data, and consequently hinders its implementation at larger scales. Thus, potential connectivity
104 metrics seem to be a sound compromise for providing reasonable estimates of functional
105 connectivity, i.e. species behavioural responses to landscape patterns (Kindlmann and Burel,
106 2008), while being applicable at large-scale due to low data requirements.

107 One promising landscape potential connectivity metric at large-scale is the metapopulation
108 capacity λ derived from metapopulation theory (Hanski and Ovaskainen, 2000). Hanski and
109 Ovaskainen defined the metapopulation as a group of spatially separated populations of the same
110 species interconnected by dispersal. In particular, the metapopulation capacity λ measures how a
111 given spatial configuration of a set of fragments contributes to the long-term persistence of a
112 particular species structured as metapopulation. This indicator has been widely used to estimate
113 the fragmentation effects in various landscapes, e.g. agricultural landscapes (Hietala-Koivu et al.,
114 2004), forest landscapes (Pardini et al., 2010; Schnell et al., 2013a), or fluvial landscapes
115 (Bertuzzo et al., 2015), and it has also been tested and explored further on simulated landscapes
116 (Grilli et al., 2015; Rybicki and Hanski, 2013). Although the metapopulation capacity λ may be a
117 promising indicator of landscape fragmentation, for now its use is limited to specific local
118 landscapes. The aim of this paper is to develop an easily appropriable and parsimonious
119 methodology to derive worldwide regionalised fragmentation indexes based on λ and to
120 demonstrate the applicability and interest of this methodology with a dispersal distance of 1 km
121 fitting a wide variety of species on all forest ecoregions in the *biodiversity hotspots* (Myers et al.,
122 2000; Russell A. Mittermeier et al., 2004) as they are the richest and the most threatened plant
123 and animal life reservoirs on Earth (Conservation International, 2016). This preliminary
124 assessment will provide a global overview of the current abilities of birds or mammals with
125 dispersal distances around 1 km to persist in the hotspots, which can be very useful in

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

130 **2. Materials and methods**

131 We used spatially explicit metapopulation models (Hanski, 1998; Hanski and Ovaskainen,
132 2000; Ovaskainen and Hanski, 2001) to describe habitat fragmentation at regional scales (e.g.
133 ecoregion scale), since the metapopulation capacity λ can conveniently be used to rank different
134 fragmented landscapes in terms of their capacity to support viable metapopulations. This section
135 will present 1) the conventional metapopulation capacity calculation at the landscape scale and
136 then 2) a methodology to extend it to large regions.

137 *2.1. Metapopulation capacity of a species in a single landscape*

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

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

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

147 $f(d_{ij}) = \max\{e^{-\alpha d_{ij}}, 0.01\}$ (2)

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

161 *2.2. Computing statistics on λ_{self} calculated at the grid square scale for a large region*

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

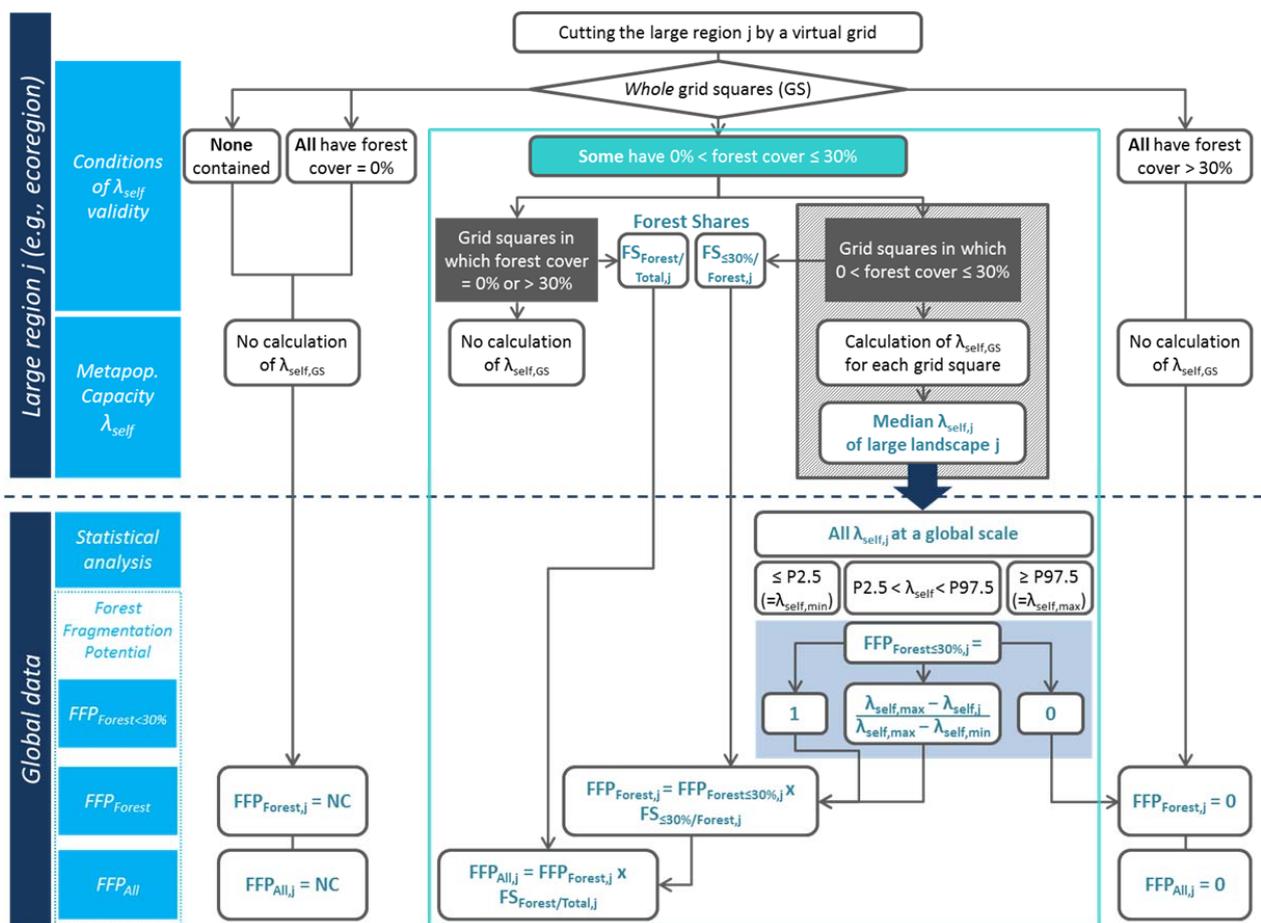
170 Thus, to compute λ_{self} for larger areas, we divided the entire region of interest by a virtual grid
171 and calculated $\lambda_{self,GS}$ for selected Grid Squares (GS) (see Figure A1 in Appendix A). The
172 landscape structure was characterised by a nonhabitat *matrix* surrounding native habitat
173 fragments. Using Q-GIS (QGIS Development Team, 2017), the habitat fragment centroids were
174 identified, and the data necessary to calculate $\lambda_{self,GS}$ were extracted, i.e. each fragment size A_i ,
175 and its centroid coordinates X_i , Y_i . The distances d_{ij} between the fragment centroids within each
176 grid square were calculated, then, by introducing the dispersal distances of the modelled species,
177 $\lambda_{self,GS}$ was calculated according to equation 1 (see Appendix A, Section 1-E for programming
178 details).

179 2.3. Deriving fragmentation indexes for large regions based on $\lambda_{self,GS}$ statistics

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

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

193 Based on $\lambda_{self,GS}$ values of all grid squares in which forest cover ranges from $>0\%$ to $\leq 30\%$ —
 194 thereafter referred to as ‘highly converted forest’—, we can determine a median value $\lambda_{self,j}$ of the
 195 non-normally distributed $\lambda_{self,GS}$ (Figure A2 in Appendix A), that stands for the metapopulation
 196 capacity of the whole large region j most converted forest areas (grey box in [Figure 1](#) [Figure 1](#)).
 197



198
 199 Figure 1: Methodology for calculating the fragmentation indexes (*Forest Fragmentation*
 200 *Potential FFP*) of a large region at three levels of spatial aggregation (highly converted forest,
 201 forest and the entire region). P: Percentile. NC: Not calculated.

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

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

216 $FFP_{Forest \leq 30\%,j}$ indicates the fragmentation ‘state’ of the most critical forest areas within region
 217 j . The more region j is fragmented, the smaller is $\lambda_{self,j}$ and the higher is $FFP_{Forest \leq 30\%,j}$:

$$218 \quad FFP_{Forest \leq 30\%,j} = \frac{(\lambda_{self,max} - \lambda_{self,j})}{(\lambda_{self,max} - \lambda_{self,min})} \quad (3)$$

219 To characterise the Forest Fragmentation Potential of the whole region $FFP_{Forest,j}$, we weight
 220 $FFP_{Forest \leq 30\%,j}$ by the proportion between the highly converted forest grid squares and the total
 221 number of forest grid squares in region j $FS_{\frac{\leq 30\%}{FOREST},j}$:

$$222 \quad FFP_{Forest,j} = FFP_{Forest \leq 30\%,j} \times FS_{\frac{\leq 30\%}{FOREST},j} \quad (4)$$

$$223 \quad \text{With } FS_{\frac{\leq 30\%}{FOREST},j} = \frac{\sum \text{GS, with } 0\% < \text{forest cover} \leq 30\%}{\sum \text{GS, with } 0\% < \text{forest cover} \leq 100\%}$$

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

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

$$229 \quad FFP_{All,j} = FFP_{Forest,j} \times FS_{\text{TOTAL},j}^{\text{FOREST}} \quad (5)$$

$$230 \quad \text{With } FS_{\text{TOTAL},j}^{\text{FOREST}} = \frac{\sum \text{GS, with } 0\% < \text{forest cover} \leq 100\%}{\sum \text{GS}}$$

231 *2.4. Implementing the methodology on forest ecoregions included in the biodiversity* 232 *hotspots*

233 For a global implementation, we first focus our assessment on the biodiversity hotspots. To
234 qualify as a biodiversity hotspot, a region must meet two criteria, i.e. 1) holding high numbers of
235 endemic vascular plants, and 2) having 30% or less of its original vegetation (Conservation
236 International, 2016), thus corresponding to the ‘fragmentation threshold’ mentioned above,
237 below which considering fragmentation is relevant. Furthermore, Sloan et al. (2014) recently
238 provided updated estimates of natural, intact vegetation within these hotspots that show that their
239 state could be even more critical than previously described. We considered all ecoregions
240 included in the biodiversity hotspots with a focus on forest major habitat types (see Appendix A,
241 Section 1–B for more details). Area loss in forests is rarely simply the removal of contiguous
242 areas and these habitats are particularly experiencing fragmentation (Whitmore and Sayer, 1992),
243 mainly because of industrial timber extraction, agricultural expansion, fire, and resource
244 extraction (Potapov et al., 2017). Due to fragmentation, the number of intact forest landscapes
245 (larger than 500 km²) is decreasing drastically, around 7% in 13 years, particularly in tropical
246 regions (Potapov et al., 2017). Thus, forests are under pressure like never before, while they host
247 90% of terrestrial species (WWF, 2016b).

248 | We applied the methodology developed (~~Figure 1~~) to all biodiversity hotspots that
249 | contain forest ecoregions (i.e. 34 forest hotspots: six in Africa, fourteen in Asia-Pacific, four in
250 | Europe and Central Asia, five in North and Central America, and five in South America). 259
251 | ecoregions met the conditions for $\lambda_{self,j}$ calculation (see *Conditions of λ_{self} validity* in ~~Figure~~
252 | ~~1~~), and FFP_j were provided for a total of 283 ecoregions, because fragmentation indexes
253 | of the 24 ecoregions for which all whole grid squares had a forest cover higher than 30% were
254 | set to 0 (see right side of ~~Figure 1~~). Details on spatial processing can be found in
255 | Appendix A, Section 1–D.

256 | 2.5. *Input data for model parameters*

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

262 | Species data are essential for the metapopulation capacity model. Provided that ‘forest’ is its
263 | habitat, a species can be heavily or slightly affected depending on its ability to move ($1/\alpha$, in
264 | connection with d_{ij}), and on its immigration and extinction abilities (x and y , related to A_i).
265 | Various ‘dispersal distances’ are reported in literature, e.g. the median, mean and maximum
266 | dispersal distances, and the migratory distance. The differences between these variables are hard
267 | to capture because their calculation varies depending on the author. Furthermore, there is a large
268 | variability associated with species dispersal distances, depending on their size or migratory
269 | habits. Based on a literature review of available species dispersal distances (Sutherland et al.,
270 | 2000), we arbitrarily considered a 1 km dispersal distance, which can apply to some birds and

271 mammals, as a first example of the methodology application. Regarding scaling factors x and y ,
272 Hanski et al. (2013) give a x realistic value for birds and mammals (1.5), while Schnell et al.
273 (2013b) propose another value valid for many taxa (0.5). Both studies considered a y value of 1.
274 We used the values provided by Schnell et al. (2013b) because they offer a broader choice in
275 terms of applications to different taxa.

276 The fragmentation assessment strongly depends on the land cover of interest definition
277 (Riitters et al., 2000). In this work, we used Globcover 2009 maps (Bontemps et al., 2011),
278 produced by the European Space Agency, which count 22 land cover classes. Among them,
279 several classes can be included in the forest definition, and considering only class 50 *Closed*
280 ($>40\%$) *broadleaved deciduous forest (>5m)*, both classes 50 and 40 *Closed to open (>15%)*
281 *broadleaved evergreen or semi-deciduous forest (>5m)*, or all eight potential forest classes
282 combined, can have a large influence on the results, underestimating or overestimating the real
283 forest cover. Furthermore, reports usually describe the remaining original habitat area in
284 percentage ‘of its original extent’ (CEPF, 2016; Di Bitetti et al., 2003), but all the ecoregion was
285 not necessarily covered with this original habitat (other land covers, water bodies, mountains,
286 etc.). To simplify our methodology, we considered all Globcover 2009 forest classes.

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

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

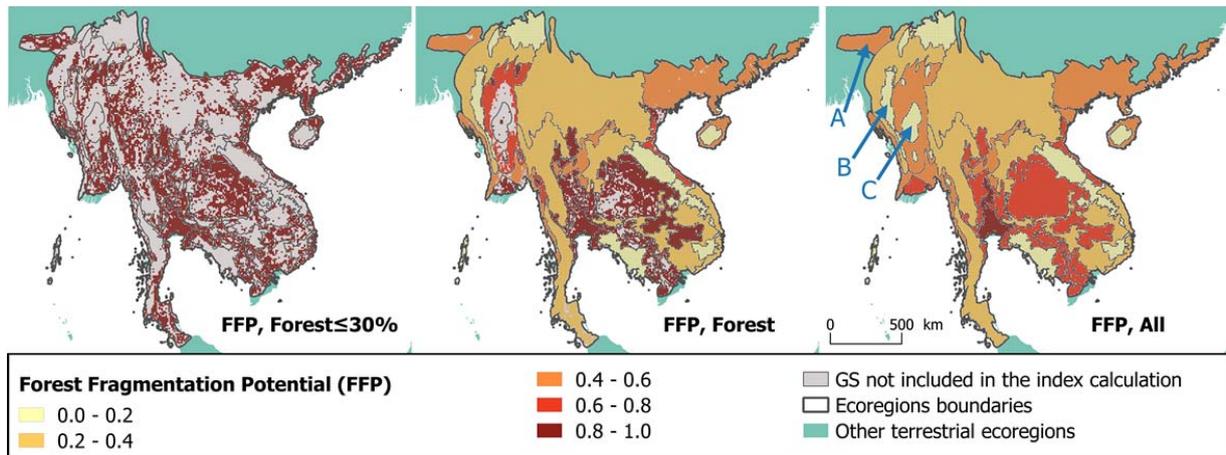
297 Likewise, fragmentation can turn out greater when larger grid sizes are used (Riitters et al.,
298 2000). Consequently, to perform a meaningful metapopulation capacity calculation, it is essential
299 to define spatial scale(s) at which metapopulation processes predominantly take place. Olson et
300 al. (2001) examined a moth metapopulation with a measured dispersal distance of 100 m at four
301 levels of spatial analysis and concluded that metapopulation processes were important at the
302 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
303 respectively). Consequently, for dispersal distances ranging from 500 m to 5 km, spatial scales
304 between 50 and 2000 km^2 would be consistent, with associated resolutions ranging from 250 m
305 to 5 km. Following the same logic as for map resolution, we could also have scaled-up the grid
306 size for λ_{self} calculations based on Hanski et al. (2013), but we found 100 km^2 more adapted to
307 the range of ecoregion sizes. 1000 km^2 grid squares were too large to adequately reflect some
308 small ecoregions, e.g. for the *Montane Fynbos And Renosterveld* ecoregion (AT1203), only three
309 grid squares were larger than 950 km^2 , representing only 6% of the whole ecoregion area. Thus,
310 a 100 km^2 -grid was applied to each hotspot, and grid squares larger than 95 km^2 (5% margin)
311 were selected for each ecoregion. Consequently, all ecoregions smaller than the grid square size
312 (100 km^2) were excluded from the outset, representing less than 0. 2% in surface of all forest
313 ecoregions belonging to the biodiversity hotspots.

314 **3. Results**

315 *3.1. Spatial representation of the three FFPs*

316 The $FFPs$ of all 30 ecoregions included in the Indo-Burma hotspot are spatially represented for
317 each 100-km² grid square included in the hotspot ([Figure 2Figure 4](#)). $FFP_{Forest \leq 30\%j}$ is a median
318 value of the most critical forest areas fragmentation ‘state’ within the ecoregion j , thus only grid
319 squares in which forest cover is smaller than 30% are concerned (upper-map in [Figure 2Figure](#)
320 [4](#)). $FFP_{Forest \leq 30\%}$ can be used to assess the potential impact on biodiversity of a current or future
321 activity using land in a highly converted forest area. As FFP_{Forest} weights the previous index by
322 the total forest cover in the ecoregion, the index value is affected to all forest grid squares
323 (middle-map in [Figure 2Figure 4](#)). FFP_{Forest} can be used to compare activities for which land use
324 surely occurs in a forest area, with no additional information on the forest cover. Lastly, FFP_{All}
325 applies to all grid squares in the ecoregion (lower-map in [Figure 2Figure 4](#)) and can be used to
326 rank land use impacts in different ecoregions when the exact locations of activities in the
327 ecoregions are unknown. The more spatially aggregated the fragmentation indexes (from
328 $FFP_{Forest \leq 30\%}$, then FFP_{Forest} , to finally FFP_{All}), the more uncertain they are.

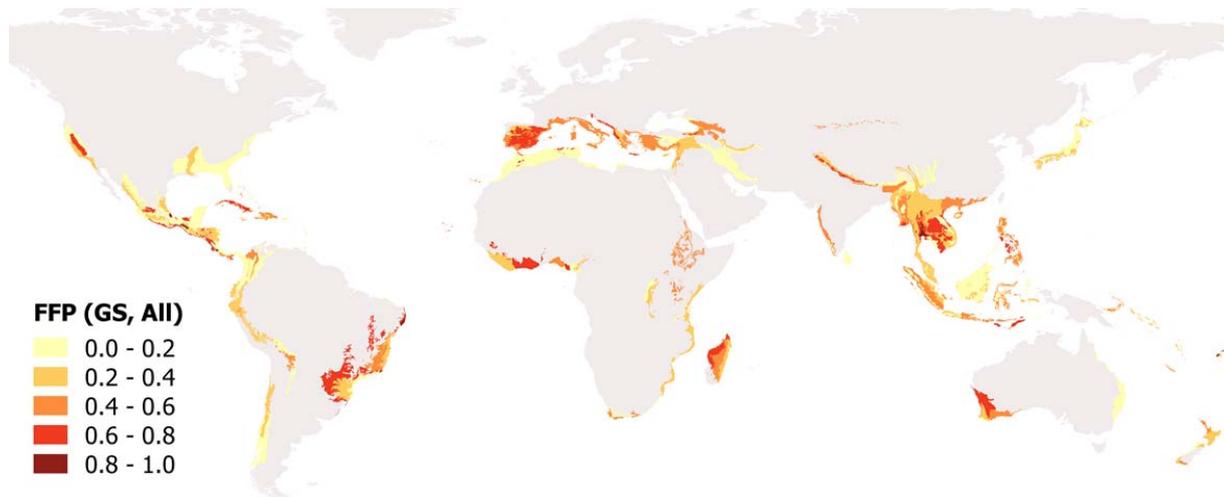
329 More explanations on the different indexes are given with the example of the Indo-Burman
330 ecoregions A, B and C ([Figure 2Figure 4](#)). All three ecoregions have a high $FFP_{Forest \leq 30\%}$
331 (respectively 0.92, 0.82 and 0.99), which means that their most converted forest zones are highly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



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

344 3.2. Global maps of FFPs

345 The fragmentation indexes were calculated for each forest ecoregion included in the 34
346 biodiversity hotspots for an illustrative species dispersal distance of 1 km. Global map of FFP_{All}
347 is presented in [Figure 3](#), and equivalent maps for $FFP_{Forest \leq 30\%}$ and FFP_{Forest} are
348 displayed in Figure A3 and Figure A4 in Appendix A. All raw data for $FFP_{Forest < 30\%}$, FFP_{Forest}
349 and FFP_{All} can be found in Appendix B (separate Excel file).



350

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

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

359 FFP_{Forest} , i.e. $FFP_{Forest \leq 30\%}$ weighted by the proportion of highly converted forest zones
360 compared to all forest zones, provides more distributed results globally (Figure A4 in Appendix
361 A). Only 22 ecoregions, mainly in Indo-Burma, Mediterranean Basin and Irano-Anatolian
362 hotspots, present FFP_{Forest} higher than 0.90. In addition, there are strong differences between
363 $FFP_{Forest \leq 30\%}$ and FFP_{Forest} results (respective median values of 0.86 and 0.27), which indicate
364 that fragmentation is most frequently a process confined to relatively specific geographical areas.
365 For instance, some ecoregions have highly fragmented forests (high $FFP_{Forest \leq 30\%}$), but only over

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

368 FFP_{All} , weighted in proportion to ecoregion forest areas, has values very similar to FFP_{Forest}
369 (global median of 0.23). This is because there are few landscapes (100 km² grid squares) with no
370 forest at all (i.e. the forest share $FS_{\frac{FOREST}{TOTAL}}$ often approaches 1), which is expected for ecoregions
371 with forest as major habitat types. Nevertheless, for some ecoregions, e.g. for the four North
372 African ecoregions included in the *Mediterranean Basin* hotspot, FFP_{Forest} can be high and
373 FFP_{All} much lower, due to their small forest cover. Conversely, e.g. in Indonesia or South
374 America, both FFP_{Forest} and FFP_{All} can be high because of some ecoregions large forest share.
375 Only three ecoregions have FFP_{All} higher than 0.9, and they all are in the *Neotropical* realm
376 (ecoregions NT0233 *Veracruz Dry Forests*, NT0102 *Atlantic Coast Restingas* and NT0151
377 *Pernambuco Coastal Forests*).
378

379 **4. Discussion**

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

391 *4.1. Metapopulation model limitations*

392 The interest of metapopulation theory to explain variations in species occurrence patterns in
393 highly fragmented landscapes has been recognised. However, metapopulation theory implies that
394 the populations exist in patchy distributions. When there is no evidence for metapopulation
395 dynamics in a given species or region, this approach might not be valid. As a great range of
396 dispersal models are available in the literature, the more adapted and realistic dispersal functions
397 $f(d_{ij})$ should be incorporated in spatial models when possible (Travis and French, 2000). In the
398 proposed methodology, due to the metapopulation model flexibility, other more complex
399 dispersal functions could easily replace the proposed one if needed. Furthermore, because

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

402 Modelling metapopulation dynamics is a very useful tool for conservation ecology. However,
403 metapopulation models have historically treated a landscape as a collection of habitat patches —
404 in our case, forest—separated by a homogenous, permeable but unsuitable habitat usually called
405 *matrix*—in our case, non-forest—. In these models, movement between patches depends only on
406 the distance between patches and the inherent species dispersal ability, and the matrix structure
407 and quality effects on movement through the landscape are neglected. Yet, even if theoretical
408 and empirical evidence show that matrix quality can be extremely important in determining
409 metapopulation dynamics (Vandermeer and Carvajal, 2001), these factors are rarely incorporated
410 into metapopulation models. In particular, linear infrastructure such as road networks can
411 considerably hinder species movements (often referred to as the ‘barrier effect’ in ecology
412 (Forman and Alexander, 1998)) and have a strong negative impact on species (Loro et al., 2015).
413 Moreover, this barrier effect varies among species, which are not similarly affected by a given
414 barrier. Gebauer et al. (2013) investigated the importance of matrix type for metapopulation
415 modelling and found that it had as much or sometimes more influence than patch sizes or
416 distances between patches on metapopulation parameters. The use of mathematical tools enabled
417 by the matrix-modelling framework, such as sensitivity and elasticity analyses (Shima et al.,
418 2010), or the incorporation of a matrix resistance parameter, which is expected to vary among
419 species (Ricketts, 2001), could definitively improve metapopulation modelling. If matrix quality
420 was to be included in the metapopulation model, complementary road maps could be used in
421 addition to Globcover 2009 maps to capture the barrier effects induced by linear infrastructure.

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

426 *4.2. Data availability and uncertainty*

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

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

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

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

464 4.3. *Applicability*

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

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

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

486 *4.4. Conclusions and perspectives*

487 The global forest fragmentation is a critical issue facing major challenges for the biodiversity
488 conservation and ecosystems management, particularly in tropical environments (Bregman et al.,
489 2014), and especially since these effects may be worsened by other global changes caused by
490 human activity, e.g. climate change (Haddad et al., 2015). Macro-scale conservation planning

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

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

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

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

528

529 **Appendices**

530 Appendix A: Additional methods and results (PDF)

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

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