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1 **How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes:**  
2 **a literature review**

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20 **Abstract**

21 Context. Landscape connectivity plays a key role in determining the persistence of species  
22 inhabiting fragmented habitat patches. In dynamic landscapes, most studies measure connectivity  
23 at multiple time steps, but pay less attention to explicitly quantifying its temporal dynamics to gain  
24 insights into its role in biodiversity patterns, thereby enabling more effective operational outcomes.

25 Objectives. This article aimed at making an overview of the existing methods for the assessment  
26 of the temporal dynamics of connectivity. By analysing their differences and possible applications,  
27 we aimed to highlight knowledge gap and future research directions.

28 Methods. We conducted a systematic review of literature dealing with the assessment of the  
29 temporal dynamics of connectivity and obtained 32 studies.

30 Results. We presented two main approaches based on graph theory and compared them from  
31 conceptual and operational perspectives. The first widely used approach, accounting only for the  
32 spatial dispersal of organisms, quantifies temporal changes in spatial connectivity. Based on two  
33 or multiple time steps in the time series, this approach enables assessment of the sense and  
34 magnitude of the temporal changes in spatial connectivity. The second recently developed  
35 approach quantifies spatio-temporal connectivity, thus accounting for both spatial and temporal  
36 dispersal. So far, this holistic assessment of spatio-temporal connectivity only covers two time  
37 steps.

38 Conclusion. Existing methods for the assessment of the temporal dynamics of connectivity provide  
39 indicators to advance our understanding of biodiversity patterns, and to be able to implement  
40 measures to conserve and restore connectivity. We propose future directions to develop these  
41 methods.

42 Keywords: temporal changes, spatial connectivity, spatio-temporal connectivity, graph theory,  
43 dispersal

## 44 **1. Introduction**

45 Landscapes are inherently dynamic both in space and over time (Sprugel 1991; Turner et al. 1993).  
46 In recent decades, anthropogenic disturbances, particularly urbanisation and agricultural  
47 intensification, have led to major changes in the type, use and spatial distribution of land cover  
48 (Fahrig et al. 2011), thus affecting landscape composition and configuration. These changes in land  
49 cover have caused habitat fragmentation per se (i.e., the breaking apart of the habitat patches,  
50 Fahrig, 2003) resulting in biodiversity loss (Haddad et al. 2015; Fletcher et al. 2018).

51 In landscapes where habitats are fragmented, species are patchily distributed in a set of local  
52 populations forming a metapopulation (Opdam 1991; Hanski 1994) and species assemblages are  
53 structured in a set of local communities forming a metacommunity (Wilson 1992; Leibold et al.  
54 2004). In this context, dispersal is an important driver of the maintenance of species populations  
55 and assemblages, because it enables the exchange of individuals among local populations and  
56 communities. Dispersal is affected by landscape connectivity, defined as the degree to which the  
57 landscape facilitates the movement of individuals among habitat patches (Taylor et al. 2006).  
58 However, connectivity varies over time following land cover changes (Taylor et al. 2006; Crooks  
59 and Sanjayan 2006). Because the changes occur over a wide range of hierarchically nested spatial  
60 and temporal scales (O'Neill et al. 1986; Allen and Starr 1988), the temporal dynamics of  
61 connectivity range from short (e.g., inter-seasonal) to long (e.g., from inter-annual to inter-decadal)  
62 time scales. Faced with these temporal dynamics of connectivity, some species react immediately  
63 whereas others respond with a time-lag (Ovaskainen and Hanski 2002; Kuussaari et al. 2009). A  
64 time-lagged response of species or assemblages to connectivity loss may reflect a relaxation time,  
65 resulting in extinction debt (Diamond 1972; Tilman et al. 1994; Kuussaari et al. 2009). Conversely,  
66 a time-lagged response of species or assemblages to connectivity gain may reflect immigration lag,  
67 resulting in immigration credit (Kuussaari et al. 2009; Jackson and Sax 2010) (**Fig. 1**). Accounting

68 for the temporal dynamics of connectivity in biodiversity studies is consequently important,  
69 especially for biodiversity conservation actions, but is often overlooked.

70 The dynamic “nature” of connectivity remains generally neglected or at best, implicit.  
71 Over the past two decades, studies have focused on the time-lagged responses of biodiversity to  
72 connectivity changes, by investigating whether past connectivity explains current species  
73 distributions better than current connectivity (for a review of time-lagged response to landscape  
74 changes, see Lira et al. 2019). Past and current connectivity were assessed using a spatial  
75 connectivity index that accounts for the spatial dispersal of organisms. This index is calculated  
76 from snapshots of the landscape, often two time steps that represent the landscape before and after  
77 the assumed change in connectivity. Biodiversity is then analysed in response of a set of different  
78 indices calculated independently for each time step. Using this approach, time-lagged responses to  
79 connectivity have been demonstrated, primarily in plants (van Ruremonde and Kalkhoven 1991;  
80 Lindborg and Eriksson 2004; Helm et al. 2006; Naaf and Kolk 2015) but also in mammals, birds,  
81 amphibians (Metzger et al. 2009) and invertebrates (Petit and Burel 1998; Bommarco et al. 2014).  
82 This approach emphasizes the importance of past connectivity in understanding current  
83 biodiversity patterns.

84 Next, some authors pointed to the need to address the temporal dynamics of connectivity  
85 more explicitly. Quantifying the temporal dynamics of connectivity to better understand its role in  
86 current biodiversity patterns would enable effective conservation or restoration actions (Kool et al.  
87 2013; Zeigler and Fagan 2014; Lira et al. 2019). To this end, a range of methods have been  
88 attempted to measure the temporal dynamics of connectivity, thereby go beyond the investigation  
89 of time-lagged response that rely solely on a quantification of a spatial connectivity index at  
90 different time steps. This can be done by quantifying temporal changes in spatial connectivity  
91 indices calculated for different times steps or by quantifying spatio-temporal connectivity over the  
92 different time steps into a single index, that account not only for the spatial dispersal of organisms,

93 but also for the probability that organisms disperse among habitat patches over time (hereafter  
94 referred to as temporal dispersal). These approaches provide estimates of the temporal dynamics  
95 of connectivity that can be related to biodiversity patterns. To our knowledge, there is no existing  
96 work yet analysing these approaches, their outputs and their implications for the ecological  
97 understanding of population dynamics and assembly rules.

98           Here, we conducted a systematic review of literature dealing with the assessment of the  
99 temporal dynamics of connectivity. We analysed existing methods from a corpus of 32 studies, and  
100 highlighted their usefulness in understanding biodiversity patterns.

## 101 2. Main body

102 We used Web of Science and Google Scholar to gather literature devoted to the assessment of the  
103 temporal dynamics of connectivity up to April 2020, and identified a total of 32 studies meeting  
104 our criteria (for more details on Methods, see **Appendix S1**). Our literature review showed that the  
105 methods to assess the temporal dynamics of landscape connectivity are all rooted in the same  
106 theoretical background, graph theory, applied to landscape ecology. We can divide them into two  
107 main approaches: (i) the quantification of temporal changes in spatial connectivity, which only  
108 accounts for spatial dispersal (94% of the papers) and (ii) the quantification of the spatio-temporal  
109 connectivity, which accounts for both spatial and temporal dispersal (6% of the papers) (see **Table**  
110 **1** for a detailed synthesis). Graph theory applied to landscape connectivity and its temporal  
111 dynamics will be described first, followed by the presentation of the two main approaches  
112 successively and their related methods. Then, we compared the differences between the two main  
113 approaches from a conceptual and operational perspective.

### 114 *2.1 Theoretical background: graph theory*

115 Urban and Keitt (2001) introduced graph theory to landscape ecologists as a modelling  
116 framework to assess landscape connectivity. In this framework, the landscape is viewed as a graph  
117 composed of a set of nodes corresponding to favourable habitat patches, connected by edges  
118 representing potential ecological fluxes (e.g., dispersal) among nodes. The nodes and edges can be  
119 weighted by the size or quality of the habitat patches and by the distance between the patches,  
120 respectively, to better represent their contribution to connectivity. The edges can be weighted by  
121 Euclidean distance, least-cost distance (Adriaensen et al. 2003) or resistance distance (McRae  
122 2006). Euclidean distance is rooted in a binary representation of the landscape (i.e., habitat patches  
123 vs uniform matrix), which assumes that organisms disperse along straight lines between two nodes  
124 (Forman and Godron 1986). By contrast, the distances resulting from least-cost paths or circuit  
125 theory acknowledge that matrix heterogeneity is an important factor in determining the dispersal

126 of organisms (Ricketts 2001). In this framework, a wide range of indices has been developed to  
127 quantify spatial connectivity at different levels, including local connectivity for characterising the  
128 elements comprising the graph (i.e., nodes or edges) and global connectivity, for characterising the  
129 entire graph (for reviews, see Galpern et al. 2011; Rayfield et al. 2011; Laita et al. 2011). The  
130 temporal dynamics of landscape connectivity is due to the occurrence of disturbances. Disturbances  
131 lead to changes in habitat patches (i.e., patch turnover), which in turn leads to changes in the degree  
132 of potential dispersal among favourable habitat patches. Landscape graphs are thus the right tool  
133 to model landscape dynamics and hence to assess the temporal dynamics of connectivity in  
134 prospective or retrospective studies. More specifically, the temporal dynamics of connectivity can  
135 be predicted or evaluated by simulating virtual changes under different scenarios or by analysing  
136 real changes to the nodes and/or edges that make up landscape graphs.

137         The first applications of graph theory to landscape modelling used spatial graphs, which  
138 meant only temporal changes in spatial connectivity could be modelled. Recent advances  
139 underlined the relevance of spatio-temporal graphs, in which nodes and edges are represented in  
140 both space and time in a multiple-layer graph (Dale 2017). This approach combines layers  
141 representing the spatial graph at each time step of the time series studied and the temporal edges  
142 between layers. This makes it possible to transpose the spatio-temporal properties of graphs in a  
143 landscape perspective that is useful for the assessment of spatio-temporal connectivity (Rayfield  
144 2009; Fletcher and Fortin 2018).

145         Whatever the type of landscape graph used, the impact of the temporal dynamics of  
146 connectivity on biodiversity can be either assumed or tested. This dichotomy is found in all studies  
147 of connectivity using landscape graphs (Foltête et al. 2020). The first set of studies investigates the  
148 temporal dynamics of connectivity without testing their effects on biodiversity. In these studies,  
149 the impact of the temporal dynamics of connectivity on biodiversity is assumed, based on the  
150 hypothesis that landscape graphs used for connectivity assessment accurately represent the



151 presence and the dispersal movements of the species concerned (see for instance Bishop-Taylor et  
152 al. 2015; Liu et al. 2017; Huang et al. 2020). The second set of study goes further thanks to  
153 empirical testing (Metzger et al. 2009; Bommarco et al. 2014; Huber et al. 2017; Raatikainen et al.  
154 2018; Horváth et al. 2019) – and sometimes, to validation (Metzger et al. 2009; Bommarco et al.  
155 2014; Raatikainen et al. 2018; Horváth et al. 2019) – of the impact of temporal dynamics of  
156 connectivity on biodiversity patterns.

## 157 *2.2 Quantification of temporal changes in spatial connectivity using multiple spatial* 158 *landscape graphs*

159 The quantification of temporal changes in spatial connectivity relies on the comparison of spatial  
160 connectivity indices computed from a sequence of spatial landscape graphs, representing snapshots  
161 of the landscape at two (**Fig. 2a**) or multiple (**Fig. 2b**) time step in the time series.

### 162 2.2.1 Two time steps in the time series

163 The first set of studies (i.e., 17 out of 30 papers) analysed the temporal changes in spatial  
164 connectivity between two time steps: before ( $t_{before}$ ), and after ( $t_{after}$ ) the assumed change in  
165 connectivity (**Fig. 2a**). The temporal changes were assessed by analysing variations before and  
166 after the loss or gain in spatial connectivity (**Fig. 3a**). Originally, this approach was used to assess  
167 the relative contribution of a given node or edge to the global connectivity, by computing the loss  
168 in global connectivity after the removal of the element concerned (e.g., Keitt et al. 1997; Rothley  
169 and Rae 2005; Matisziw and Murray 2009; Bodin and Saura 2010; Rubio et al. 2015). The variation  
170 in global connectivity was transposed to a more temporal perspective, for instance to enable  
171 conservation or restoration measures to be applied to specific patches (García-Feced et al. 2011) or  
172 landscapes (Rappaport et al. 2015). For instance, Rappaport et al. (2015) proposed an “urgency  
173 indicator” based on the differences in the amount of habitat and global connectivity between  $t_{before}$   
174 and  $t_{after}$  to enable prioritisation of the landscapes to be protected or restored. These authors

175 differed markedly in their ranking of forest landscapes to be restored or conserved whether both  
176 the sense and the magnitude of changes in habitat cover and connectivity between 1990 and 2002  
177 were taken into account. This suggests that prioritisation of landscapes to be restored or conserved  
178 may be hampered by disregarding landscape dynamics.

179         The analysis of variations in spatial connectivity have also been used to understand how  
180 land cover changes affect the temporal changes in spatial connectivity, often at global scale  
181 (Baudry et al. 2003; Saura et al. 2011, 2019; Liu et al. 2014, 2017; Mazaris et al. 2013; Sahraoui  
182 et al. 2017; Mui et al. 2017), and sometimes at the local scale (Mazaris et al. 2013; Mui et al. 2017).  
183 For instance, Liu et al. (2017) tested the effect of forest plantation expansion on global spatial  
184 connectivity of natural forests. They reported that connectivity loss varied from 55% to 96%  
185 between 1972 and 2012, depending on the degree of forest plantation expansion in three of the four  
186 areas they studied, while the gain in connectivity was 2% over the same period in areas where no  
187 forests were planted. Other authors, including Horváth et al. (2019), went further by testing the  
188 effect on biodiversity of the variation in local spatial connectivity between 1957 and 2010. In  
189 temporary ponds subject to up to 70% of habitat loss, these authors showed that the greater the loss  
190 of local connectivity, the greater the loss of invertebrate zooplankton richness over the period  
191 concerned. However, they focused on changes in spatial connectivity between two time steps,  
192 without investigating whether the loss or gain in connectivity was significant; e.g., by testing  
193 whether the mean value of connectivity differed statistically between  $t_{before}$  and  $t_{after}$ . By  
194 contrast, through the use of the standard error of the mean and statistical tests, respectively,  
195 Bommarco et al. (2014) and Huber et al. (2017) demonstrated significant losses of local  
196 connectivity of grasslands before analysing whether a time-lagged response in biodiversity had  
197 taken place.

198         Overall, assessing temporal changes in spatial connectivity based on variations in spatial  
199 connectivity at two time steps is a simple, time-saving and affordable method to assess whether

200 (significance), how (sense) and to what extent (magnitude) connectivity values have changed or  
201 could change over time. Since this variation is based on two time steps, the assessment of temporal  
202 changes in spatial connectivity assumes that connectivity changes in a purely linear way over time.  
203 However, additional changes in connectivity may occur between the two time steps, particularly  
204 during long time series. Studying these changes may provide deeper insights into biodiversity  
205 patterns. The use of a higher temporal resolution with multiple time steps  $t_x$  over the time series  
206 studied ( $t_{before} < t_x < t_{after}$ ) should thus improve the assessment of temporal changes in spatial  
207 connectivity.

## 208 2.2.2 Multiple time steps $t_x$ in the time series

### 209 2.2.2.1 Visual examination of the curve representing spatial connectivity values

210 Among studies based on multiple time steps over the time series (i.e., 13 out of 30 papers; **Fig. 2b**),  
211 those focusing on graph robustness (i.e., the number of elements that can be removed without  
212 altering global connectivity; Minor and Urban 2008) were probably the first to visually examine  
213 the curve of global spatial connectivity over successive deletions of nodes or edges (e.g., Urban  
214 and Keitt 2001). Originally used to study the sensitivity of global connectivity to disturbances, this  
215 approach has been transposed to a more temporal perspective (**Fig. 3b-1**). For instance, Tulbure et  
216 al. (2014) investigated how the global connectivity of aquatic habitat patches might change in a  
217 warmer climate, assumed to lead to aquatic habitat patch loss. They assessed the robustness of the  
218 aquatic landscape by studying the curve of global connectivity with an increasing proportion of  
219 sequentially removed aquatic habitat patches. Other authors go further, reporting a visual  
220 examination of the temporal changes in spatial connectivity accounting for changes in nodes and/or  
221 and edges at both global (Bishop-Taylor et al. 2015; Saura et al. 2019) and local (Metzger et al.  
222 2009; Raatikainen et al. 2018) scales. For example, Bishop-Taylor et al. (2015) considered global  
223 spatial connectivity of surface water habitats under eight flooding scenarios ranging from no flood

224 to a 100-year average recurrence interval in an aquatic landscape. They found that the flooding  
225 recurrence interval was positively correlated with global connectivity, suggesting that flooding  
226 creates a “transient connectivity window” (Zeigler and Fagan 2014), i.e., a period during which  
227 matrix conditions increase the probability of successful individual movement between habitat  
228 patches.

229 Although the use of curves provides a better overview of the temporal changes in spatial  
230 connectivity than values measured at successive time steps in the time series, it remains a purely  
231 descriptive indicator quantifying the sense and the magnitude of the temporal changes in spatial  
232 connectivity.

#### 233 2.2.2.2 Assessment of variations in spatial connectivity values

234 Above and beyond visual examination of the curve of spatial connectivity over multiple time steps,  
235 it is possible to extend the approach based on the variation of spatial connectivity values before  
236 and after an assumed change in connectivity to multiple time steps in the time series (**Fig. 3b-2**).  
237 In this case, the simulations of land cover changes correspond to a virtual time represented by a  
238 series of events without reference to a precise date. This approach has been used to identify  
239 appropriate locations for connectivity measures (Foltête et al. 2014; Clauzel et al. 2015; Foltête  
240 2018). Foltête et al. (2014) investigated the gain in global connectivity over 10 successive additions  
241 of wildlife crossings in a pond network for amphibian species as a criterion to identify the location  
242 of each new wildlife crossing to be added in order to maximize global connectivity. Nevertheless,  
243 the investigation of the variation of connectivity over multiple time steps has mainly been used to  
244 study temporal changes in spatial connectivity as changes in land cover occur. For instance,  
245 Metzger et al. (2009) assessed the changes in local connectivity values in three successive time  
246 steps (1962, 1981, 2000). These changes over successive–decades were assessed using two  
247 indicators for each habitat patch: the differences in connectivity between 1962 and 1981 and  
248 between 1981 and 2000. Interestingly, they provided the first and so far, the only evidence that past

249 connectivity (1962 and/or 1981) and/or the successive temporal changes in connectivity (1962-  
250 1981 and/or 1981-2000) explain the current diversity patterns of trees, frogs and birds. Similar  
251 approaches were applied by Hernández et al. (2015), McIntyre et al. (2018) and Saura et al. (2019),  
252 who used variations in global and/or local spatial connectivity over several time steps to assess  
253 temporal changes in the spatial connectivity of forest, aquatic habitats and protected areas over  
254 long time periods (1975-2011, 1945-2000s and 2010-2018), respectively. McIntyre et al. (2018)  
255 averaged connectivity values obtained from numerous short time steps (e.g., intra-decadal) to a few  
256 long time steps (e.g., inter-decadal). However, averaging may conceal notable variability of  
257 connectivity values over time which could be crucial for aquatic biodiversity, as shown by Tulbure  
258 et al. (2014) and Bishop-Taylor et al. (2018) (see section 2.2.2.3).

259 By contrast, several studies tested for significant differences in local or global connectivity  
260 between time steps in the time series. These differences were assessed by comparing the standard  
261 error (Rayfield et al. 2008; Raatikainen et al. 2018) or the 95% confidence interval (Bishop-Taylor  
262 et al. 2015) around mean connectivity values. Statistical tests could be also used though already  
263 done yet. For instance, Rayfield et al. (2008) analysed temporal changes in global spatial  
264 connectivity of forest habitat patches in four time steps over a 200-year time series according to  
265 five scenarios of protection of the patches. Applying ten replicates of each scenario, they averaged  
266 the global connectivity of forest patches for each time step. By reporting the initial connectivity  
267 and the average connectivity coupled to its standard error obtained at each time step on a plot, they  
268 demonstrated that global connectivity decreased in most of the scenarios investigated.

269 To go further, especially if many time steps are involved, it is possible to use statistical  
270 modelling to identify the sign and the magnitude of the overall trend of connectivity values, while  
271 accounting for the variability of connectivity values occurring over the period concerned.

272 2.2.2.3 Assessment of the overall trend of spatial connectivity values using statistical analysis

273 Although indicators derived from statistical modelling of the relationship between time and  
274 connectivity can accurately assess temporal changes in spatial connectivity in multiple time steps,  
275 their use remains rare (**Fig. 3b-3**). To our knowledge, only two studies have used trend analysis to  
276 assess the temporal changes in spatial connectivity (Tulbure et al. 2014; Bishop-Taylor et al.  
277 2018a). Tulbure et al. (2014) analysed global connectivity values of aquatic habitat patches for 278  
278 time steps over a 13-year time series. Using a Mann-Kendall trend test, these authors reported that  
279 global connectivity was subject to high seasonal variability while significantly decreasing over the  
280 whole period, suggesting potential consequences for species inhabiting these aquatic habitats.  
281 Extending the use of statistical analysis to assess the overall trend of spatial connectivity values at  
282 multiple time steps is probably the most promising quantitative and precise approach for the  
283 assessment of temporal changes in spatial connectivity. The relationship between time and  
284 connectivity can be explored, for instance, through linear, logarithmic, exponential polynomial or  
285 power functions. Assessing trends in spatial connectivity at multiple time steps makes it possible  
286 to determine not only the significance and the sense of the overall temporal changes in spatial  
287 connectivity but also the magnitude of the changes.

288 Overall, the use of multiple time steps provides a finer assessment of the temporal changes  
289 in spatial connectivity before and after an assumed change, by accounting for the inner connectivity  
290 variability between the two time steps. Including the multiple changes in connectivity that occur  
291 within a time series in the assessment of the temporal changes in spatial connectivity is particularly  
292 important to reflect the underlying ecological processes as accurately as possible. Besides the sense  
293 and magnitude of these temporal changes, their abruptness and their variability can also be assessed  
294 (**Fig. 4**). Trend analysis is a powerful but still underexploited tool to make a finer yet broader  
295 assessment of the temporal changes in spatial connectivity by means of additional indicators (e.g.,  
296 variability: standard error of the residuals; abruptness: power value  $n$  of a power function fitted to  
297 the data). Although the effects of the sense and the magnitude of the temporal changes in spatial

298 connectivity still need to be fed by evidence (but see Metzger et al. 2009; Bommarco et al. 2014;  
299 Huber et al. 2017; Raatikainen et al. 2018; Horváth et al. 2019), we recommend going further by  
300 exploring the effects of the variability and the abruptness in connectivity. These two components  
301 also likely drive the dispersal movements of organisms, and hence their response to temporal  
302 changes in spatial connectivity. The recent incorporation in the metacommunity theory of temporal  
303 variations in dispersal (Matias et al. 2013) that can result from variability in spatial connectivity  
304 may help predict biodiversity patterns. However, the importance of abruptness in dispersal changes  
305 have yet to be integrated in basic theory to yield predictions regarding biodiversity.

### 306 2.3 *The quantification of the spatio-temporal connectivity using a spatio-temporal landscape* 307 *graph*

308 The assessment of the temporal dynamics of landscape connectivity based on a sequence of spatial  
309 landscape graphs only accounts for spatial dispersal among favourable habitat patches over the  
310 time series. It has been challenged, notably by Rayfield (2009), who argued that changes in habitat  
311 patches do not only affect spatial dispersal between habitat patches at a given time step, but also  
312 the dispersal of organisms between habitat patches between time steps. Rayfield (2009) and more  
313 recently Martensen et al. (2017) and Fletcher and Fortin (2018) discussed the need to move  
314 forward, by assessing spatio-temporal connectivity using a spatio-temporal landscape graph.  
315 Transposed from a landscape perspective, a spatio-temporal graph represents a snapshot of the  
316 landscape integrating the time series. Yet, to date, spatio-temporal connectivity has only been  
317 developed for two time steps (**Fig. 2c**). Rayfield (2009) suggested that spatial and temporal edges  
318 can be weighted by the spatial distance and the duration of the time series, respectively; but this  
319 approach has not yet been explored. Martensen et al. (2017) proposed a similar method, in which  
320 spatial and temporal edges are weighted based on the probability of spatio-temporal dispersal (**Fig.**  
321 **2c**). Each node is weighted by its change over the time series, that is, by habitat patch turnover  
322 between  $t_{before}$  and  $t_{after}$ . Specifically, the node can be either gained (node absent in  $t_{before}$  but

323 present in  $t_{after}$ ), lost (node present in  $t_{before}$  but absent in  $t_{after}$ ) or remain stable (node present  
324 in  $t_{before}$  and in  $t_{after}$ ). The weight attributed to the temporal edges between nodes depends on  
325 the (possible) simultaneous existence of nodes between the time steps considered (i.e., at  $t_x$ ,  
326 between  $t_{before}$  and  $t_{after}$ ). If the two nodes exist simultaneously at  $t_x$  (e.g., if the organism  
327 disperses from a node being lost or gained to a stable node between  $t_{before}$  and  $t_{after}$ ), the weight  
328 attributed to a temporal edge is 1. If information concerning the simultaneous existence of two  
329 nodes at  $t_x$  is unknown (e.g., if the organism disperses from a node gained to a node lost between  
330  $t_{before}$  and  $t_{after}$ , or the opposite), the weight is 0.5. By multiplying the spatial and temporal  
331 weight of the edge, the probability of spatio-temporal dispersal between two habitat patches is  
332 obtained and hence a spatio-temporal connectivity index is calculated between the two time steps.

333 To date, only Martensen et al. (2017) and Huang et al. (2020) have used this framework.  
334 Martensen et al. (2017) examined the spatio-temporal connectivity before (1990) and after (2001)  
335 a hypothesised change in connectivity in a forest landscape. They compared the global connectivity  
336 of forest patches obtained from the only-spatial approach based on snapshots of the landscape at  
337 the two time steps studied, with those obtained from the spatio-temporal approach based on a  
338 snapshot of the landscape over these two time steps. Notably, they demonstrated that only-spatial  
339 connectivity can lead to an underestimation (on average 30%, but can reach 150%) of the spatio-  
340 temporal connectivity, especially in landscapes where the loss of habitat is high. Huang et al. (2020)  
341 observed similar patterns by simulating hypothetical distributions of 300 species in virtual  
342 landscapes under climate change. In particular, the spatial-temporal connectivity was higher than  
343 the only-spatial connectivity in 44% of the 300 virtual species, and underestimation occurred when  
344 loss of habitat amount, quality and isolation occurred between  $t_{before}$  and  $t_{after}$ . The authors also  
345 investigated how the ability of three “real” species to expand their range under different climate  
346 change scenarios affected underestimation of only-spatial connectivity. They found that the  
347 difference between future (2030) only-spatial connectivity and the spatio-temporal connectivity



348 measured over the time series [from the present (1970-2018) to future (2030)] declined in species  
349 that will probably expand their range, and vice versa. These studies emphasise the need to include  
350 the consequences of changes in habitat patches in the ability of an organism to reach habitat patches  
351 between two time steps to quantify the “real” (i.e., spatio-temporal) connectivity and its potential  
352 consequences for biodiversity.

353 Overall, the inclusion of both the spatial and temporal components of the dispersal processes  
354 enabled more precise quantification of connectivity in dynamic landscapes. Nevertheless, this  
355 novel approach is, so far, restricted to two time steps ( $t_{before}$  and  $t_{after}$ ) over the time series,  
356 which probably justifies the trinary weighting of temporal edges and thus a very simplified view  
357 of the process of temporal dispersal. Including multiple time steps  $t_x$  will pave the way for possible  
358 improvements to accurately fit the dispersal process of organisms, such as the (i) time and the  
359 period (e.g., linked to the state of habitat patches) required to disperse among habitat patches and  
360 (ii) the temporal scale at which organisms respond to connectivity. This would first require  
361 accounting for the duration of the (possible) simultaneous existence of two habitat patches in the  
362 spatio-temporal model of connectivity, by weighting the probability of temporal dispersal between  
363 two habitat patches as a function of the duration of their simultaneous existence (Rayfield 2009).  
364 The duration of temporal edges is indeed likely to drive the magnitude of the dispersal flux (number  
365 of individuals) but also the probability of species with low dispersal ability to disperse over time  
366 from one favourable habitat patch to another. In addition, weighting the temporal edges according  
367 to the simultaneous existence of two habitat patches in a particular state (e.g., flooding) could make  
368 it possible to account for the most suitable or required dispersal periods for the organism concerned.  
369 Further, the potential legacy effects exerted by connectivity on current biodiversity patterns need  
370 to be explicitly accounted for to reach a holistic understanding of how spatio-temporal connectivity  
371 affects existing biodiversity patterns. Adequate weighting of the spatio-temporal probability to  
372 disperse between two habitat patches between two successive time steps is one way to include the

373 time-lag curves (i.e., the degree to which species respond to connectivity at different time steps of  
374 the time series studied) in the spatio-temporal connectivity approach.

#### 375 2.4 *Conceptual and operational divergences*

376 Our literature review was rooted in the dichotomy of two main approaches (see above 2.2 and 2.3)  
377 to assess the temporal dynamics of landscape connectivity.

378 While major advances have been made in methods to assess the temporal dynamics of  
379 connectivity, it is still not clear if the two main approaches reflect the same ecological processes  
380 and answer the same questions. By accounting for spatial dispersal, the quantification of temporal  
381 changes in spatial connectivity reflects the patterns of opportunities for the dispersal of organisms  
382 at multiple time steps, but not between these time steps. Nonetheless, considering the temporal  
383 changes in spatial connectivity is one step forward in our understanding of the persistence of  
384 (meta)-populations and (meta-)communities, which so far has only been seen as determined by  
385 spatial connectivity (i.e., the degree of spatial connectivity obtained from a snapshot or an average  
386 of multiple snapshot(s) of the landscape). The magnitude, the frequency and even the duration of  
387 transient changes in spatial connectivity as drivers of the persistence of (meta)-populations and  
388 (meta)-communities were overlooked until the recent works of Perry and Lee (2019) and de  
389 Santana et al. (2015). In dynamic landscapes, habitat patch turnover may outweigh the relationships  
390 between spatial connectivity and species occupancy, even if the spatial connectivity shapes  
391 colonisation processes (Biedermann 2004; Hodgson et al. 2009). Therefore, like habitat loss  
392 (Keymer et al. 2000), spatial connectivity should be at least as important as its patterns of temporal  
393 changes – if not more so – in determining current biodiversity patterns. But patch turnover also  
394 provides spatio-temporal connectivity among patches, thereby allowing individuals to disperse  
395 among ephemeral patches over time, even though the patches are spatially isolated at any single  
396 time step (Keymer et al. 2000; Matlack and Monde 2004; Wimberly 2006). Omitting the spatio-  
397 temporal connectivity may therefore not only lead to the absence of apparent connectivity effects,

398 but also to underestimating connectivity in dynamic landscapes. Moreover, Martensen et al. (2017)  
399 modelled spatio-temporal connectivity by weighting the temporal edges as a function of the  
400 changes of patches. This implies that high patch turnover rates may result in “pulsed” release of  
401 dispersers, and influences colonisation rates and occupancy over time (Reigada et al. 2015).  
402 Overall, spatio-temporal connectivity is a promising avenue towards understanding the “real”  
403 relationships between biodiversity and connectivity in dynamic landscapes, although also limiting  
404 our predictions about whether and how spatial connectivity varies over time.

405 Our review also revealed marked differences in how the two main approaches estimate temporal  
406 dynamics of connectivity. Although the four components (sense, magnitude, variability, and  
407 abruptness) of the temporal changes in spatial connectivity can be properly estimated, spatio-  
408 temporal connectivity cannot estimate these components, since they are intrinsically embedded in  
409 the spatio-temporal connectivity itself. Only spatio-temporal connectivity provides a single holistic  
410 estimate of connectivity in space and over time, but it cannot be assessed based on multiple time  
411 steps  $t_x$  in the time series.

### 412 **3 Conclusion and prospects for future research**

413 Methods designed for the assessment of the temporal dynamics of landscape connectivity provide  
414 insights into the consequences for landscape connectivity of both natural and anthropic  
415 disturbances. They provide operational indicators to identify which specific areas (from patches to  
416 landscapes) have undergone changes in connectivity over time, or not, and to what extent these  
417 changes may affect or have affected biodiversity patterns through time-lagged or immediate  
418 responses. From this synthesis, we propose different recommendations for improving the existing  
419 methods.

420 First, considering a higher temporal resolution is needed, especially for the assessment of  
421 spatio-temporal connectivity. Today, obtaining a finer temporal resolution is easy, especially  
422 thanks to the recent development of powerful tools to (i) rapidly and accurately digitise past land  
423 cover maps, such as the HistMapR free package (Auffret et al. 2017) and (ii) obtain accurate data  
424 at a frequent time resolution to digitise current land cover maps thanks to the recent advances in  
425 remote sensing methods, accessible at low cost, coupled with efficient machine-learning algorithms  
426 (Rapinel et al. 2019). However, it is crucial to keep identical spatial resolutions and classification  
427 techniques and land cover maps completely overlaid over the time series. The methodological  
428 requirements needed to address spatio-temporal connectivity are hence hard to meet due to changes  
429 in the nature of the sensors, which necessitates to work on corrective methods that could facilitate  
430 overcoming these constraints.

431 Second, we stressed the importance of analysing the relevance of the approach chosen  
432 according to biological data. More especially, the two approaches need to be compared, jointly  
433 testing their respective effects on biodiversity. With that aim in view, future studies should bear in  
434 mind that assessing the temporal dynamics of connectivity needs to be adapted to the ecological  
435 processes studied in order to account for the processes underpinning the relationships between

436 connectivity, its temporal dynamics and biodiversity patterns. To this end, the temporal range, that  
437 is the duration of time series considered, needs to match the temporal scale of the response of the  
438 organisms studied, which is relative to their longevity, turnover rate, and dispersal capacity  
439 (Kuussaari et al. 2009; Jackson and Sax 2010).

440 Third, and lastly, future research should also keep in mind that the temporal scales of response  
441 are hierarchically nested (level of organisation), the temporal response at the individual scale being  
442 shorter than that of community scale (Hylander & Ehrlén, 2013). Existing works, even those based  
443 on multiple intra- and inter-annual time steps (Tulbure et al. 2014; Bishop-Taylor et al. 2018a),  
444 investigated the temporal dynamics of connectivity based on the time steps taken independently.  
445 These works hence omit that the short-term (e.g., intra-annual) temporal dynamics of connectivity  
446 are nested in long-term (e.g., inter-annual) dynamics.

447 Overall, the approaches reviewed in this article could provide new methods and decision-  
448 making tools for land-use planners. The difficulty in disentangling the underlying components of  
449 the temporal changes in spatial connectivity can also hamper the choice of actions to be  
450 implemented to manage connectivity in dynamic landscapes. Spatio-temporal connectivity may  
451 thus be an innovative and powerful tool for land-use planners, but ultimately, it needs to move  
452 toward a realistic and feasible indicator for setting conservation and restoration priorities. We  
453 believe that - at present - the joint use of the two approaches would allow more precautionary  
454 management of connectivity and its impacts on biodiversity. This combination of approaches could  
455 especially help prioritize specific areas to be protected or to be used to implement and test  
456 connectivity conservation or restoration measures in a dynamic perspective (i.e., “mobile”  
457 protected areas, the locations of which change over time; Bull et al. 2013) to maintain, restore and  
458 protect biodiversity in a changing world.

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471 Availability of data and material (data transparency)

472 All data analysed during this study are included in this published

473 Code availability (software application or custom code)

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475 Authors' contributions

476 Conceived the ideas and designed methodology - LU, AA, CM, AE. Analysed and  
477 interpreted the data - LU. Prepared all figures, table, appendix - LU. Led the writing of the  
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480

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706 Table 1 Synthesis of the studies devoted to the assessment of the temporal dynamics of  
707 connectivity. Studies are categorized according to the approach (Type I or II) and the method they  
708 used (A to D). Type I: quantification of the temporal changes in spatial connectivity. Type 2:  
709 quantification of spatio-temporal connectivity. A: assessment of variations in spatial connectivity  
710 values. B: assessment of variations in spatial connectivity values, tested for significant differences  
711 in connectivity values between the two time steps or among the time steps. C: visual examination  
712 of the curve representing spatial connectivity values. D: assessment of the overall trend of spatial  
713 connectivity values using statistical analysis. "-": none.

714

<b>Type of approach for assessing the temporal dynamics of landscape connectivity</b>	<b>Number of time step</b>	<b>Method</b>	<b>Time series studied</b>	<b>Connectivity scale</b>	<b>Impact of the temporal dynamics of landscape connectivity on biodiversity</b>	<b>Reference</b>
Type I	Two	A	Before and after the removal of a given element	Global	Assumed	Keitt et al. (1997)
Type I	Two	A	Before and after the removal of a given element	Global	Assumed	Rothley and Rae (2005)

Type I	Two	A	Before and after the removal of a given element	Global	Assumed	Matisziw and Murray (2009)
Type I	Two	A	Before and after the removal of a given element	Global	Assumed	Bodin and Saura (2010)
Type I	Two	A	Before and after the removal of a given element	Global	Assumed	Rubio et al. (2015)
Type I	Two	A	Spring and late summer	Global	Assumed	Mui et al. (2017)
Type I	Two	B	Spring and late summer	Local	Assumed	Mui et al. (2017)
Type I	Two	A	Before and after the reforestation of a given agricultural patch (node)	Global	Assumed	García-Feced et al. (2011)
Type I	Two	A	1990 - 2002	Global	Assumed	Rappaport et al. (2015)
Type I	Two	B	Conventional farming system and farming system undergoing intensification of production	Global	Assumed	Baudry et al. (2003)
Type I	Two	A	1990 - 2000	Global	Assumed	Saura et al. (2011)
Type I	Two	A	1991 - 2006	Global	Assumed	Liu et al. (2014)
Type I	Two	A	1976 - 2012	Global	Assumed	Liu et al. (2017)

Type I	Two	A	Current and future distributions of species under scenarios of both land use and climate change	Global	Assumed	Mazaris et al. (2013)
Type I	Two	B	Current and future distributions of species under scenarios of both land use and climate change	Local	Assumed	Mazaris et al. (2013)
Type I	Two	A	1982 - 2012	Global	Assumed	Sahraoui et al. (2017)
Type I	Two	A	1957 - 2010	Local	Tested. Result: the greater the loss of local connectivity, the greater the loss of local invertebrate zooplankton richness over the period.	Horvath et al. (2019)
Type I	Two	B	1950's - 2000's	Local	Tested. Result: a significant loss of connectivity was observed, and a time-lagged response to connectivity was	Bommarco et al. (2014)



					demonstrated on (specialist and generalist) plant and (specialist) butterfly richness.	
Type I	Two	B	1830 - 2013	Local	Tested. Result: a significant loss of connectivity was observed, but no time-lagged response to connectivity was demonstrated on plant richness	Huber et al. - (2017)
Type I	Multiple: (i) 50 node and (ii) $n$ edges removals	C	None - (i) 50 nodes and (ii) $n$ edges removal (depending on the threshold distance applied)	Global	Assumed	Urban and Keitt (2001)
Type I	Multiple: 1 to 30 % (in increments of 1%) node removals in relation to the total number of nodes in the graph	C	1 - 30% of the nodes sequentially removed in the graph	Global	Assumed	Tulbure et al. (2014)
Type I	Multiple: 278 time steps	D	1999 - 2011	Global	Assumed	Tulbure et al. (2014)
Type I	Multiple: 8 flooding scenarios (no flooding and	C	No flooding - 100 year average	Global	Assumed	Bishop-Taylor et al. (2015)

	1, 2, 5, 10, 20, 50, and 100 year average recurrence interval floods)		recurrence interval floods			
Type I	Multiple: 8 flooding scenarios (no flooding and 1, 2, 5, 10, 20, 50, and 100 year average recurrence interval floods)	B	No flooding - 100 year average recurrence interval floods	Local	Assumed	Bishop-Taylor et al. (2015)
Type I	Multiple: 3 (1962, 1981, 2000)	C + A	1962 - 2000	Local	Tested. Results: past connectivity (1962 and/or 1981) and the successive variations in spatial connectivity values (1962-1981 and/or 1981-2000) explain the current diversity patterns of trees, frogs and birds.	Metzger et al. (2009)
Type I	Multiple: 3 (mid-19 <sup>th</sup> , late-20 <sup>th</sup> , early 21 <sup>st</sup> centuries)	C + B	mid-19 <sup>th</sup> century - early 21 <sup>st</sup> century	Local	Tested. Result: A loss of connectivity was observed. Time-	Raatikainen et al. (2018)

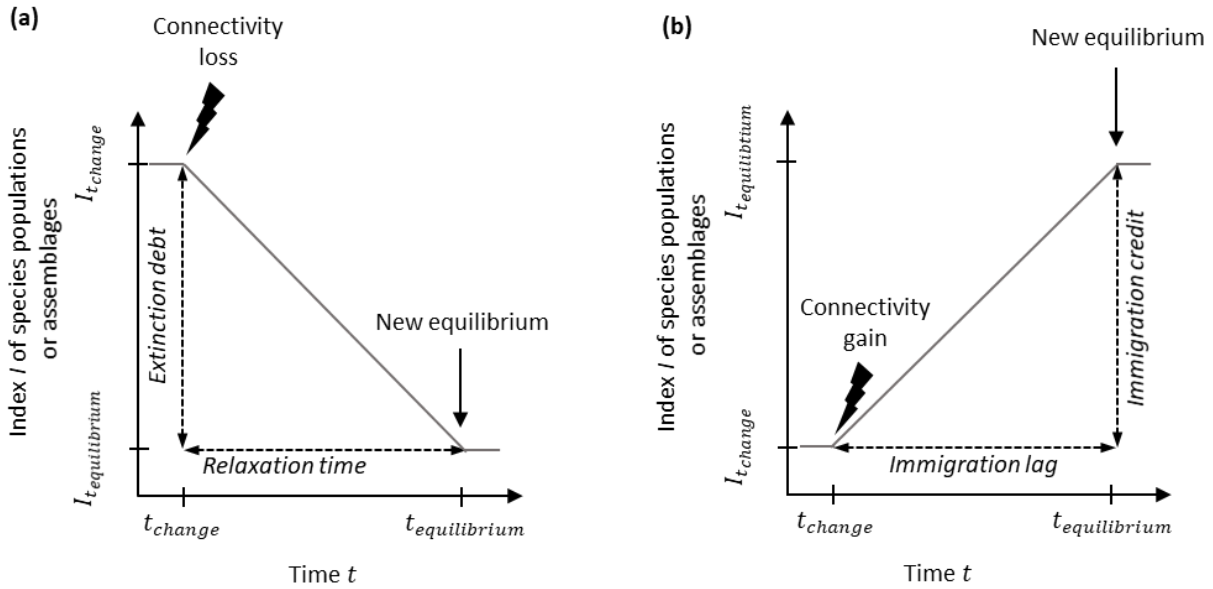
					lagged responses to connectivity were demonstrated for plant abundance but not for plant richness.	
Type I	Multiple: ten successive (i) ponds (nodes) and (ii) wildlife crossing (edges) additions	A	None - (i) ten ponds (nodes) and (ii) ten wildlife crossing additions	Global	Assumed	Foltête et al. (2014)
Type I	Multiple: ten successive ponds (nodes) additions	A	None to ten ponds (nodes) additions	Global	Assumed	Clauzel et al. (2015)
Type I	Multiple: 20 and all $n$ habitat patches (nodes) removals or converted into another land-cover	A	None - (i) 20 and (ii) all $n$ habitat patches (nodes) removal or converted into another land-cover	Global	Assumed	Foltête (2018)
Type I	Multiple :4 (1974, 1992, 2001, 2011)	A	1975 - 2011	Global	Assumed	Hernández et al. (2015)
Type I	Multiple: 3 (1945, 1980's and 2000's)	A	1945 – 2000's	Global and local	Assumed	McIntyre et al. (2018)
Type I	Multiple: 5 (2010, 2012, 2014, 2016 and 2018)	C + A	2010 - 2018	Global	Assumed	Saura et al. (2019)

Type I	Multiple: 5 [0 (initial conditions) and 50, 100, 150, 200 years of 5 alternative protected areas (patches) scenarios]	B	0 - 200-year simulation of forest dynamics	Global	Assumed	Rayfield et al. (2008)
Type I	Multiple: 99 time steps	D	1987 - 2011	Global	Assumed	Bishop-Taylor et al. (2018)
Type II	Two	-	1990 - 2001	Global	Assumed	Martensen et al. (2017)
Type II	Two	-	Current and future climate scenarios	Global	Assumed	Huang et al. (2020)

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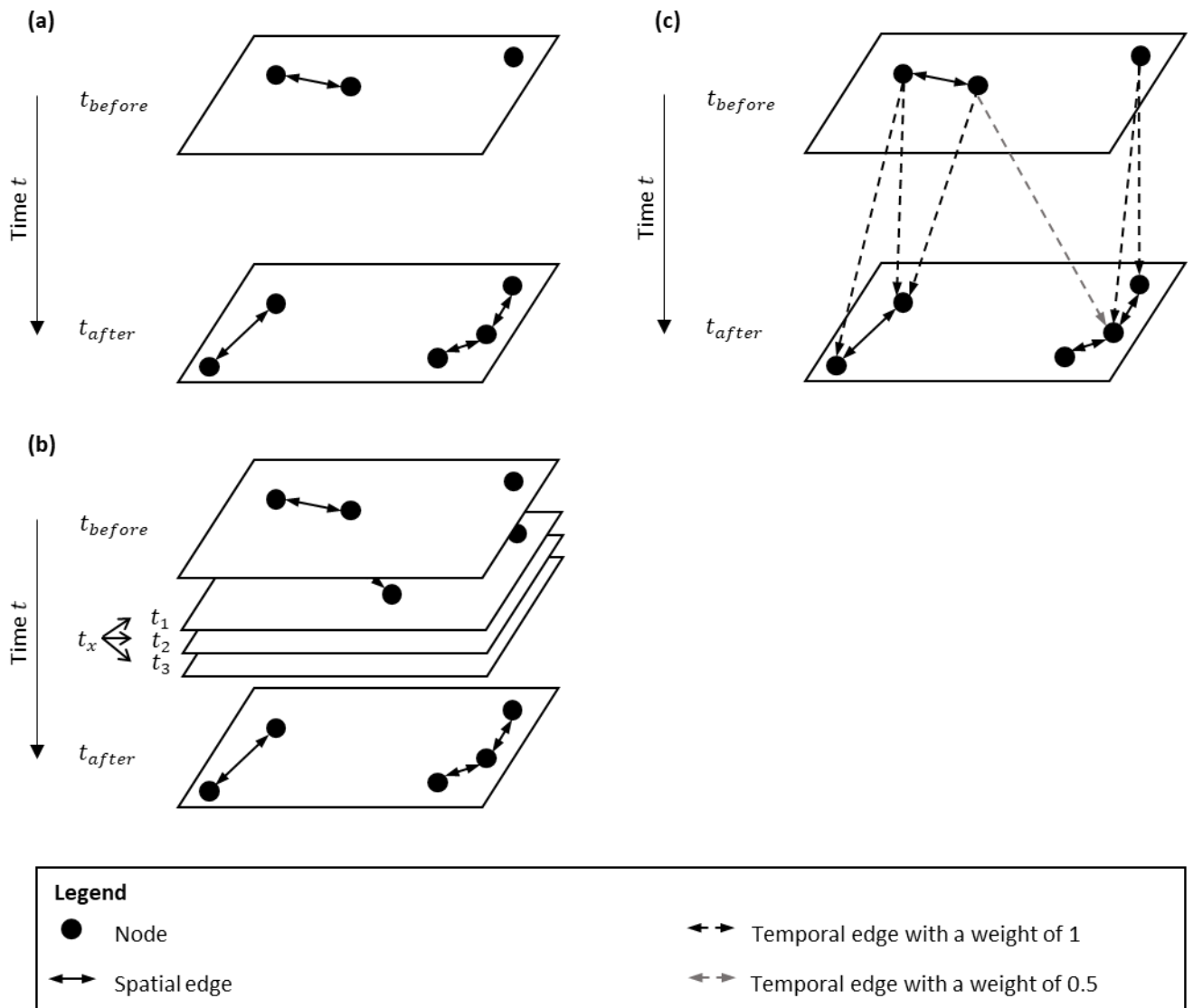
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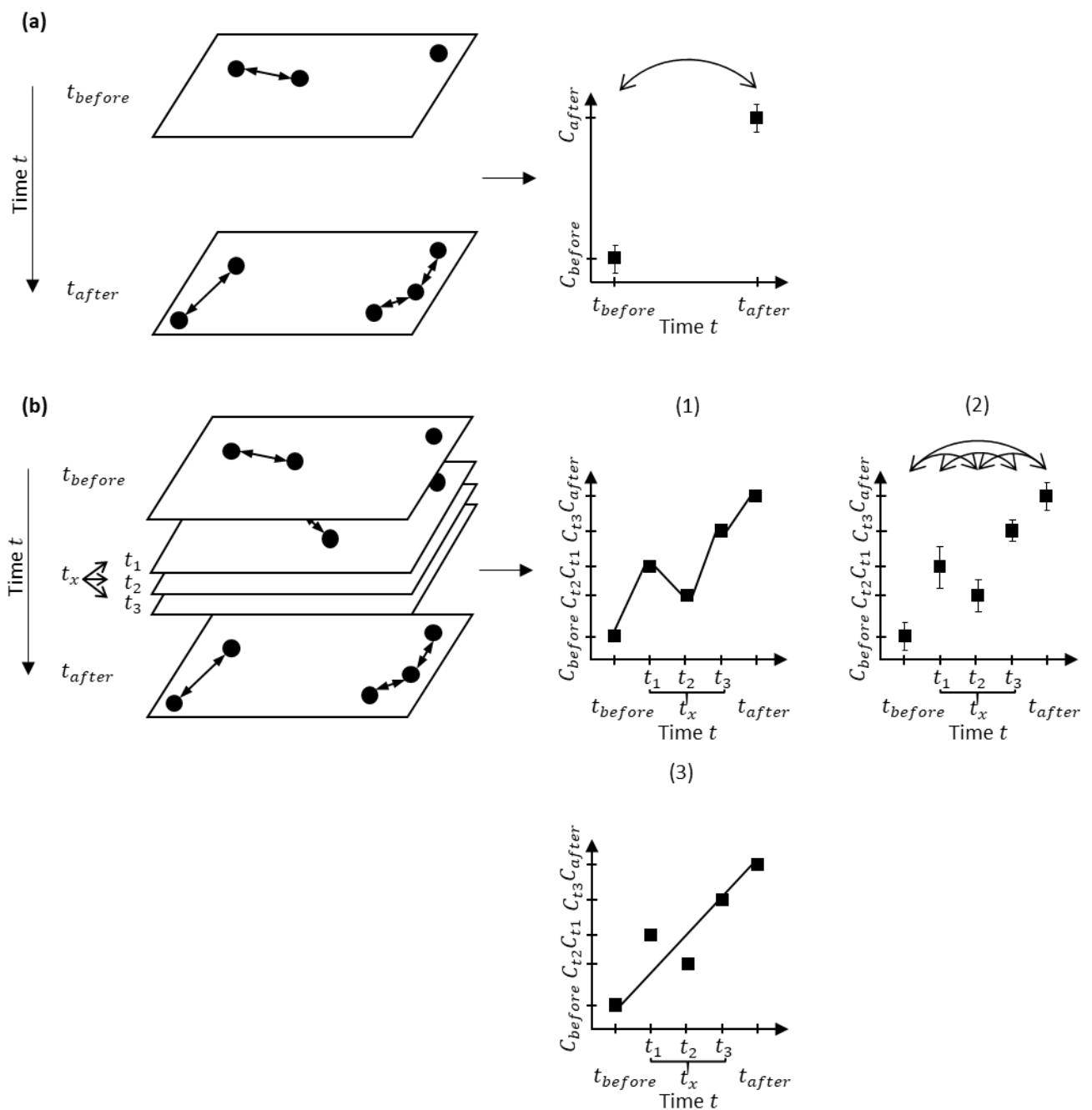
719 **Fig. 1** Illustrations of time-lagged responses and their effects on species populations or assemblages  
720 following a (a) loss or (b) gain in landscape connectivity.  $t_{change}$  is the time step at which  
721 connectivity changed (either loss or gain) and for which no response of species (either extinction  
722 or immigration) has yet taken place.  $t_{equilibrium}$  is the time step at which species response has  
723 occurred and a new equilibrium has been reached.  $I_{t_{change}}$  and  $I_{t_{equilibrium}}$  are an index  $I$  describing  
724 either species populations (e.g., presence, density) or assemblages (e.g., species richness, diversity)  
725 at  $t_{change}$  and  $t_{equilibrium}$ , respectively. Adapted from Hylander and Ehrlén (2013).



726

727 **Fig. 2** The temporal dynamics of landscape connectivity can be assessed from spatial landscape  
 728 graphs (left) either for (a) two time steps of the time series [i.e., before ( $t_{before}$ ), and after  
 729 ( $t_{after}$ )] the change in connectivity or (b) multiple time steps  $t_x$  ( $t_{before} < t_x < t_{after}$ ) or from a  
 730 spatio-temporal landscape graph (right) for (c) two time steps of the time series, that is with  
 731 temporal edges running between the two spatial landscape graphs. (a) and (b) quantify the temporal  
 732 changes in spatial connectivity, by comparing two or multiple spatial connectivity indices  
 733 calculated from spatial graphs in which spatial edges connect nodes depending on the distance-  
 734 based weights attributed to edges for a given time step of the time series. (c) quantifies the spatio-  
 735 temporal connectivity using a spatio-temporal graph in which temporal edges connect nodes

736 between the two spatial graphs depending on the weights attributed to temporal edges which is  
737 based on the (possible) simultaneous existence of nodes at  $t_x$ . The simultaneous existence of nodes  
738 at  $t_x$  is function of their change between  $t_{before}$  and  $t_{after}$  (gain, loss or stable). If the two nodes  
739 exist simultaneously at  $t_x$ , the weight attributed to a temporal edge is 1. If information concerning  
740 the simultaneous existence of two nodes at  $t_x$  is unknown, the weight is 0.5. Adapted from  
741 Martensen et al. (2017).

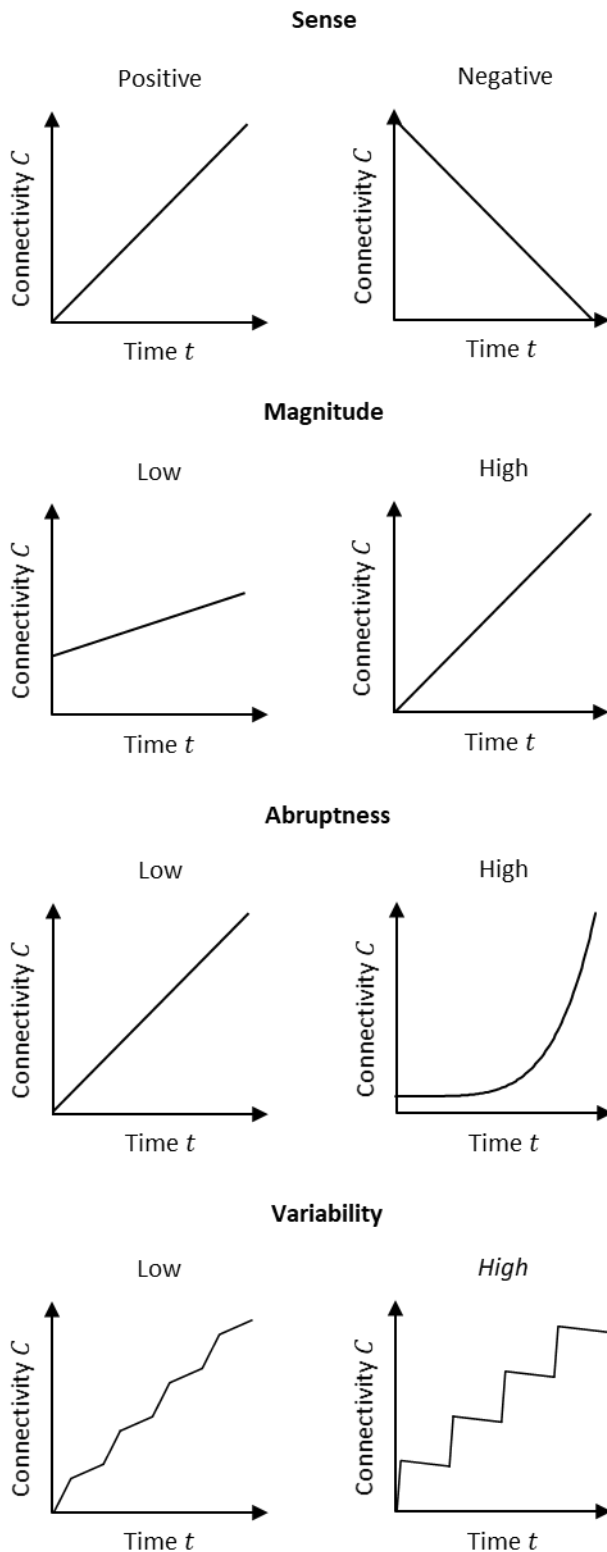


742

743 **Fig. 3** Overview of possible approaches to assess the temporal changes in spatial connectivity from  
 744 the comparison of multiple spatial connectivity indices, calculated independently for different time  
 745 steps in the time series. Such temporal changes can be assessed with **(a)** two time steps in the time  
 746 series [i.e., before ( $t_{before}$ ) and after ( $t_{after}$ ) the change in connectivity] by assessing the variation  
 747 in spatial connectivity values or **(b)** multiple time steps  $t_x$  ( $t_{before} < t_x < t_{after}$ ) by (1) visually  
 748 examining the curve of spatial connectivity values, (2) assessing the variation in spatial



749 connectivity values or (3) assessing the overall trend of spatial connectivity values using statistical  
750 analysis.



751

752 **Fig. 4** Overview of the different components of the temporal changes in spatial connectivity that  
 753 could be provided by statistical modelling of the relationship between time and connectivity (trend  
 754 analysis). Indicators derived from statistical analysis could infer the sense (i.e., positive or negative

755 connectivity changes over the time series), the magnitude (i.e., the strength at which connectivity  
756 changes over the time series), the abruptness (i.e., the sharpness at which connectivity changes over  
757 the time series) and the variability (i.e., the alternation of time steps with high connectivity and  
758 time steps with low connectivity over the time series) of temporal changes in spatial connectivity.

759 **Appendix S1 Methods**

760 We reviewed articles to identify the currently existing methods that aim to assess the temporal  
761 dynamics of landscape connectivity. We interrogated Web of Science and Google Scholar with the  
762 following keywords: “landscape connect\*”, “temporal”, “time”, “dynamics”, “changes” and  
763 “variability” to compiled peer-reviewed papers (excluding review papers) that were published up  
764 until April 2020. On the basis of the titles and abstracts, we focused on papers which reserved the  
765 use of the “graph theory” term in a landscape perspective to focus on landscape connectivity *per*  
766 *se*. We read the methodology section of each paper and excluded papers that did not mention the  
767 use for estimating the temporal dynamics of landscape connectivity. We supplemented the few  
768 papers we found with additional studies from the reference section of these papers. Methods that  
769 were solely used in a single study were then excluded (e.g., Hermoso et al. 2012; Ruiz et al. 2014;  
770 Bishop-Taylor et al. 2018b). Overall, we identified a total of 32 studies.