

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

Léa Uroy, Audrey Alignier, Cendrine Mony, Jean-Christophe Foltête, Aude Ernoult

► To cite this version:

Léa Uroy, Audrey Alignier, Cendrine Mony, Jean-Christophe Foltête, Aude Ernoult. How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. Landscape Ecology, 2021, 36 (9), pp.2487-2504. 10.1007/s10980-021-01277-9. hal-03337527

HAL Id: hal-03337527 https://hal.inrae.fr/hal-03337527

Submitted on 15 Sep 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

- **1** How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes:
- 2 a literature review
- 3 Léa Uroy^{1,2*}, Audrey Alignier², Cendrine Mony¹, Jean-Christophe Foltête³, Aude Ernoult¹.
- 4 1: UMR 6553 ECOBIO, CNRS, University of Rennes, Avenue du Général Leclerc, 35042 Rennes
- 5 Cedex, France
- 6 2: UMR 0980 BAGAP, INRAE, Institut Agro, 65 Rue de Saint-Brieuc, 35042 Rennes Cedex,
 7 France
- 8 3: UMR 6049 ThéMA, CNRS, University Bourgogne Franche-Comté, 32 Rue Mégevand, 25030
- 9 Besançon, France
- 10 *: <u>lea.uroy@univ-rennes1.fr</u>
- 11 ORCID iD
- 12 Léa Uroy: 0000-0003-4967-4017
- 13 Audrey Alignier: 0000-0002-7619-7124
- 14 Cendrine Mony: 0000-0002-0061-6521
- 15 Jean-Christophe Foltête: 0000-0003-4864-5660
- 16 Aude Ernoult: 0000-0003-4654-0072
- 17 Acknowledgements
- 18 This work was funded by the Fondation de France (BISCO project). We thank Daphné Goodfellow
- 19 for the English editing.



20 Abstract

Context. Landscape connectivity plays a key role in determining the persistence of species 21 inhabiting fragmented habitat patches. In dynamic landscapes, most studies measure connectivity 22 23 at multiple time steps, but pay less attention to explicitly quantifying its temporal dynamics to gain insights into its role in biodiversity patterns, thereby enabling more effective operational outcomes. 24 Objectives. This article aimed at making an overview of the existing methods for the assessment 25 of the temporal dynamics of connectivity. By analysing their differences and possible applications, 26 we aimed to highlight knowledge gap and future research directions. 27 28 Methods. We conducted a systematic review of literature dealing with the assessment of the temporal dynamics of connectivity and obtained 32 studies. 29 30 Results. We presented two main approaches based on graph theory and compared them from conceptual and operational perspectives. The first widely used approach, accounting only for the 31 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

magnitude of the temporal changes in spatial connectivity. The second recently developed
approach quantifies spatio-temporal connectivity, thus accounting for both spatial and temporal
dispersal. So far, this holistic assessment of spatio-temporal connectivity only covers two time
steps.

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

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

44 1. Introduction

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

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

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

The dynamic "nature" of connectivity remains generally neglected or at best, implicit. 70 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 distributions better than current connectivity (for a review of time-lagged response to landscape 73 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 from snapshots of the landscape, often two time steps that represent the landscape before and after 76 77 the assumed change in connectivity. Biodiversity is then analysed in response of a set of different indices calculated independently for each time step. Using this approach, time-lagged responses to 78 connectivity have been demonstrated, primarily in plants (van Ruremonde and Kalkhoven 1991; 79 Lindborg and Eriksson 2004; Helm et al. 2006; Naaf and Kolk 2015) but also in mammals, birds, 80 amphibians (Metzger et al. 2009) and invertebrates (Petit and Burel 1998; Bommarco et al. 2014). 81 82 This approach emphasizes the importance of past connectivity in understanding current biodiversity patterns. 83

84 Next, some authors pointed to the need to address the temporal dynamics of connectivity more explicitly. Quantifying the temporal dynamics of connectivity to better understand its role in 85 current biodiversity patterns would enable effective conservation or restoration actions (Kool et al. 86 2013; Zeigler and Fagan 2014; Lira et al. 2019). To this end, a range of methods have been 87 attempted to measure the temporal dynamics of connectivity, thereby go beyond the investigation 88 of time-lagged response that rely solely on a quantification of a spatial connectivity index at 89 90 different time steps. This can be done by quantifying temporal changes in spatial connectivity indices calculated for different times steps or by quantifying spatio-temporal connectivity over the 91 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.

Here, we conducted a systematic review of literature dealing with the assessment of the
temporal dynamics of connectivity. We analysed existing methods from a corpus of 32 studies, and
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 temporal dynamics of connectivity up to April 2020, and identified a total of 32 studies meeting 103 104 our criteria (for more details on Methods, see Appendix S1). Our literature review showed that the methods to assess the temporal dynamics of landscape connectivity are all rooted in the same 105 theoretical background, graph theory, applied to landscape ecology. We can divide them into two 106 107 main approaches: (i) the quantification of temporal changes in spatial connectivity, which only accounts for spatial dispersal (94% of the papers) and (ii) the quantification of the spatio-temporal 108 connectivity, which accounts for both spatial and temporal dispersal (6% of the papers) (see Table 109 110 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 successively and their related methods. Then, we compared the differences between the two main 112 approaches from a conceptual and operational perspective. 113

114 *2.1 Theoretical background: graph theory*

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

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

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

Whatever the type of landscape graph used, the impact of the temporal dynamics of connectivity on biodiversity can be either assumed or tested. This dichotomy is found in all studies of connectivity using landscape graphs (Foltête et al. 2020). The first set of studies investigates the temporal dynamics of connectivity without testing their effects on biodiversity. In these studies, the impact of the temporal dynamics of connectivity on biodiversity is assumed, based on the hypothesis that landscape graphs used for connectivity assessment accurately represent the presence and the dispersal movements of the species concerned (see for instance Bishop-Taylor et
al. 2015; Liu et al. 2017; Huang et al. 2020). The second set of study goes further thanks to
empirical testing (Metzger et al. 2009; Bommarco et al. 2014; Huber et al. 2017; Raatikainen et al.
2018; Horváth et al. 2019) – and sometimes, to validation (Metzger et al. 2009; Bommarco et al.
2014; Raatikainen et al. 2018; Horváth et al. 2019) – of the impact of temporal dynamics of
connectivity on biodiversity patterns.

157

158

2.2 Quantification of temporal changes in spatial connectivity using multiple spatial landscape graphs

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

162

2.2.1 <u>Two time steps in the time series</u>

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

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

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

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

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

208

2.2.2 <u>Multiple time steps t_x in the time series</u>

209 2.2.2.1 Visual examination of the curve representing spatial connectivity values

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

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

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

233 2.2.2.2 Assessment of variations in spatial connectivity values

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

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

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

To go further, especially if many time steps are involved, it is possible to use statistical modelling to identify the sign and the magnitude of the overall trend of connectivity values, while 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

Although indicators derived from statistical modelling of the relationship between time and 273 274 connectivity can accurately assess temporal changes in spatial connectivity in multiple time steps, their use remains rare (Fig. 3b-3). To our knowledge, only two studies have used trend analysis to 275 276 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 time steps over a 13-year time series. Using a Mann-Kendall trend test, these authors reported that 278 279 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 connectivity can be explored, for instance, through linear, logarithmic, exponential polynomial or 284 power functions. Assessing trends in spatial connectivity at multiple time steps makes it possible 285 to determine not only the significance and the sense of the overall temporal changes in spatial 286 connectivity but also the magnitude of the changes. 287

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

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

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

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

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

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

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

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

375 2.4 *Conceptual and operational divergences*

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

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

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

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

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

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

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

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

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

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

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

459 **Declarations**

460	Funding (information that explains whether and by whom the research was supported)
461	This work was funded by the Fondation de France (BISCO project).
462	Conflicts of interest/Competing interests (include appropriate disclosures)
463	The authors have no financial or proprietary interests in any material discussed in this
464	article.
465	Ethics approval (include appropriate approvals or waivers)
466	Not relevant
467	Consent to participate (include appropriate statements)
468	Not relevant
469	Consent for publication (include appropriate statements)
470	All authors gave their consent for publication.
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)
474	Not relevant
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
478	manuscript - LU. Contributed critically to drafting and revising the manuscript - LU, AA, CM,
479	JCF, AE. Final approval for publication - LU, AA, CM, JCF, AE.
480	

481 **References**

- Adriaensen F, Chardon JP, De Blust G, et al (2003) The application of 'least-cost' modelling as a
 functional landscape model. Landsc Urban Plan 64:233–247.
 https://doi.org/10.1016/S0169-2046(02)00242-6
- Allen TFH, Starr TB (1988) Hierarchy: Perspectives for Ecological Complexity. University of
 Chicago Press, Chicago
- Auffret AG, Rico Y, Bullock JM, et al (2017) Plant functional connectivity integrating landscape
 structure and effective dispersal. J Ecol. https://doi.org/10.1111/1365-2745.12742
- Baudry J, Burel F, Aviron S, et al (2003) Temporal variability of connectivity in agricultural
 landscapes: do farming activities help? Landsc Ecol 18:303–314
- Biedermann R (2004) Modelling the spatial dynamics and persistence of the leaf beetle Gonioctena
 olivacea in dynamic habitats. Oikos 107:645–653. https://doi.org/10.1111/j.00301299.2004.13358.x
- Bishop-Taylor R, Tulbure MG, Broich M (2015) Surface water network structure, landscape
 resistance to movement and flooding vital for maintaining ecological connectivity across
 Australia's largest river basin. Landsc Ecol 30:2045–2065. https://doi.org/10.1007/s10980 015-0230-4
- Bishop-Taylor R, Tulbure MG, Broich M (2018a) Impact of hydroclimatic variability on regional scale landscape connectivity across a dynamic dryland region. Ecol Indic 94:142–150.
 https://doi.org/10.1016/j.ecolind.2017.07.029
- Bishop-Taylor R, Tulbure MG, Broich M (2018b) Evaluating static and dynamic landscape
 connectivity modelling using a 25-year remote sensing time series. Landsc Ecol 1–16.
 https://doi.org/10.1007/s10980-018-0624-1
- Bodin Ö, Saura S (2010) Ranking individual habitat patches as connectivity providers: Integrating
 network analysis and patch removal experiments. Ecol Model 221:2393–2405.
 https://doi.org/10.1016/j.ecolmodel.2010.06.017
- Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower visiting insects in landscapes with contrasting land use history. Divers Distrib 20:591–599.
 https://doi.org/10.1111/ddi.12187
- Bull JW, Suttle KB, Singh NJ, Milner-Gulland E (2013) Conservation when nothing stands still:
 moving targets and biodiversity offsets. Front Ecol Environ 11:203–210.
 https://doi.org/10.1890/120020
- Clauzel C, Bannwarth C, Foltête J-C (2015) Integrating regional-scale connectivity in habitat
 restoration: An application for amphibian conservation in eastern France. J Nat Conserv
 23:98–107. https://doi.org/10.1016/j.jnc.2014.07.001
- 516 Crooks KR, Sanjayan M (2006) Connectivity Conservation. Cambridge University Press

517 Dale MRT (2017) Spatio-temporal Graphs. In: Applying graph theory in ecological research, 1st 518 edn. Cambridge University Press, Cambridge, pp 222–251

- de Santana CN, Klecka J, Palamara GM, Melián CJ (2015) Metacommunity in dynamic
 landscapes. bioRxiv 021220. https://doi.org/10.1101/021220
- 521 Diamond JM (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of
 522 southwest pacific islands. Proc Natl Acad Sci 69:3199–3203.
 523 https://doi.org/10.1073/pnas.69.11.3199
- Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst
 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
- Fahrig L, Baudry J, Brotons L, et al (2011) Functional landscape heterogeneity and animal
 biodiversity in agricultural landscapes. Ecol Lett 14:101–112.
 https://doi.org/10.1111/j.1461-0248.2010.01559.x
- Fletcher R, Fortin M-J (2018) Spatial Ecology and Conservation Modeling: Applications with R.
 Springer International Publishing
- Fletcher RJ, Didham RK, Banks-Leite C, et al (2018) Is habitat fragmentation good for
 biodiversity? Biol Conserv 226:9–15. https://doi.org/10.1016/j.biocon.2018.07.022
- Foltête J-C (2018) A parcel-based graph to match connectivity analysis with field action in agricultural landscapes: Is node removal a reliable method? Landsc Urban Plan 178:32–42.
 https://doi.org/10.1016/j.landurbplan.2018.05.016
- Foltête J-C, Girardet X, Clauzel C (2014) A methodological framework for the use of landscape
 graphs in land-use planning. Landsc Urban Plan 124:140–150.
 https://doi.org/10.1016/j.landurbplan.2013.12.012
- Foltête J-C, Savary P, Clauzel C, et al (2020) Coupling landscape graph modeling and biological
 data: a review. Landsc Ecol. https://doi.org/10.1007/s10980-020-00998-7
- 541 Forman RTT, Godron M (1986) Landscape Ecology. Wiley
- Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: A guide to
 construction, analysis and application for conservation. Biol Conserv 144:44–55.
 https://doi.org/10.1016/j.biocon.2010.09.002
- García-Feced C, Saura S, Elena-Rosselló R (2011) Improving landscape connectivity in forest
 districts: A two-stage process for prioritizing agricultural patches for reforestation. For Ecol
 Manag 261:154–161. https://doi.org/10.1016/j.foreco.2010.09.047
- Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on
 Earth's ecosystems. Sci Adv 1:e1500052. https://doi.org/10.1126/sciadv.1500052
- Hanski I (1994) A Practical Model of Metapopulation Dynamics. J Anim Ecol 63:151–162.
 https://doi.org/10.2307/5591
- Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and
 fragmentation. Ecol Lett 9:72–77. https://doi.org/10.1111/j.1461-0248.2005.00841.x

- Hermoso V, Ward DP, Kennard MJ (2012) Using water residency time to enhance spatio-temporal
 connectivity for conservation planning in seasonally dynamic freshwater ecosystems. J
 Appl Ecol 49:1028–1035. https://doi.org/10.1111/j.1365-2664.2012.02191.x
- Hernández A, Miranda M, Arellano EC, et al (2015) Landscape dynamics and their effect on the
 functional connectivity of a Mediterranean landscape in Chile. Ecol Indic 48:198–206.
 https://doi.org/10.1016/j.ecolind.2014.08.010
- Hodgson JA, Moilanen A, Thomas CD (2009) Metapopulation responses to patch connectivity and
 quality are masked by successional habitat dynamics. Ecology 90:1608–1619.
 https://doi.org/10.1890/08-1227.1
- Horváth Z, Ptacnik R, Vad CF, Chase JM (2019) Habitat loss over six decades accelerates regional
 and local biodiversity loss via changing landscape connectance. Ecol Lett 22:1019–1027.
 https://doi.org/10.1111/ele.13260
- Huang J-L, Andrello M, Martensen AC, et al (2020) Importance of spatio-temporal connectivity
 to maintain species experiencing range shifts. Ecography 43:591–603.
 https://doi.org/10.1111/ecog.04716
- Huber S, Huber B, Stahl S, et al (2017) Species diversity of remnant calcareous grasslands in south
 eastern Germany depends on litter cover and landscape structure. Acta Oecologica 83:48–
 55. https://doi.org/10.1016/j.actao.2017.06.011
- Hylander K, Ehrlén J (2013) The mechanisms causing extinction debts. Trends Ecol Evol 28:341–
 346. https://doi.org/10.1016/j.tree.2013.01.010
- Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt,
 immigration credit and species turnover. Trends Ecol Evol 25:153–160.
 https://doi.org/10.1016/j.tree.2009.10.001
- Keitt T, Urban DL, Milne BT (1997) Detecting Critical Scales in Fragmented Landscapes. Conserv
 Ecol 1:art4. https://doi.org/10.5751/ES-00015-010104
- Keymer JE, Marquet PA, Velasco-Hernández JX, Levin SA (2000) Extinction Thresholds and
 Metapopulation Persistence in Dynamic Landscapes. Am Nat 156:478–494.
 https://doi.org/10.1086/303407
- Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. Landsc Ecol 28:165–185. https://doi.org/10.1007/s10980-012-9819-z
- Kuussaari M, Bommarco R, Heikkinen RK, et al (2009) Extinction debt: a challenge for
 biodiversity conservation. Trends Ecol Evol 24:564–571.
 https://doi.org/10.1016/j.tree.2009.04.011
- Laita A, Kotiaho JS, Mönkkönen M (2011) Graph-theoretic connectivity measures: what do they
 tell us about connectivity? Landsc Ecol 26:951–967. https://doi.org/10.1007/s10980-011 9620-4
- Leibold MA, Holyoak M, Mouquet N, et al (2004) The metacommunity concept: a framework for
 multi-scale community ecology. Ecol Lett 7:601–613. https://doi.org/10.1111/j.1461 0248.2004.00608.x

- Lindborg R, Eriksson O (2004) Historical Landscape Connectivity Affects Present Plant Species
 Diversity. Ecology 85:1840–1845. https://doi.org/10.1890/04-0367
- Lira PK, de Souza Leite M, Metzger JP (2019) Temporal Lag in Ecological Responses to
 Landscape Change: Where Are We Now? Curr Landsc Ecol Rep 4:70–82.
 https://doi.org/10.1007/s40823-019-00040-w
- Liu S, Dong Y, Deng L, et al (2014) Forest fragmentation and landscape connectivity change
 associated with road network extension and city expansion: A case study in the Lancang
 River Valley. Ecol Indic 36:160–168. https://doi.org/10.1016/j.ecolind.2013.07.018
- Liu S, Yin Y, Liu X, et al (2017) Ecosystem Services and landscape change associated with
 plantation expansion in a tropical rainforest region of Southwest China. Ecol Model
 353:129–138. https://doi.org/10.1016/j.ecolmodel.2016.03.009
- Martensen AC, Saura S, Fortin M-J (2017) Spatio-temporal connectivity: assessing the amount of
 reachable habitat in dynamic landscapes. Methods Ecol Evol 8:1253–1264.
 https://doi.org/10.1111/2041-210X.12799
- Matias MG, Mouquet N, Chase JM (2013) Dispersal stochasticity mediates species richness in
 source–sink metacommunities. Oikos 122:395–402. https://doi.org/10.1111/j.1600 0706.2012.20479.x
- Matisziw TC, Murray AT (2009) Connectivity change in habitat networks. Landsc Ecol 24:89–
 100. https://doi.org/10.1007/s10980-008-9282-z
- Matlack GR, Monde J (2004) Consequences of low mobility in spatially and temporally
 heterogeneous ecosystems. J Ecol 92:1025–1035. https://doi.org/10.1111/j.0022 0477.2004.00908.x
- Mazaris AD, Vokou D, Halley JM, et al (2016) Dynamics of extinction debt across five taxonomic
 groups. Nat Commun 7:12283. https://doi.org/10.1038/ncomms12283
- McIntyre NE, Collins SD, Heintzman LJ, et al (2018) The challenge of assaying landscape
 connectivity in a changing world: A 27-year case study in the southern Great Plains (USA)
 playa network. Ecol Indic 91:607–616. https://doi.org/10.1016/j.ecolind.2018.04.051
- 620 McRae BH (2006) Isolation by Resistance. Evolution 60:1551–1561. 621 https://doi.org/10.1111/j.0014-3820.2006.tb00500.x
- Metzger JP, Martensen AC, Dixo M, et al (2009) Time-lag in biological responses to landscape
 changes in a highly dynamic Atlantic forest region. Biol Conserv 142:1166–1177.
 https://doi.org/10.1016/j.biocon.2009.01.033
- Minor ES, Urban DL (2008) A Graph-Theory Framework for Evaluating Landscape Connectivity
 and Conservation Planning. Conserv Biol 22:297–307. https://doi.org/10.1111/j.1523 1739.2007.00871.x
- Mui AB, Caverhill B, Johnson B, et al (2017) Using multiple metrics to estimate seasonal landscape
 connectivity for Blanding's turtles (Emydoidea blandingii) in a fragmented landscape.
 Landsc Ecol 32:531–546. https://doi.org/10.1007/s10980-016-0456-9

- Naaf T, Kolk J (2015) Colonization credit of post-agricultural forest patches in NE Germany
 remains 130–230years after reforestation. Biol Conserv 182:155–163.
 https://doi.org/10.1016/j.biocon.2014.12.002
- O'Neill RV, Deangelis DL, Waide JB, Allen TFH (1986) A Hierarchical Concept of Ecosystems.
 Princeton University Press, Princeton
- Opdam P (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding
 bird studies. Landsc Ecol 5:93–106. https://doi.org/10.1007/BF00124663
- Ovaskainen O, Hanski I (2002) Transient Dynamics in Metapopulation Response to Perturbation.
 Theor Popul Biol 61:285–295. https://doi.org/10.1006/tpbi.2002.1586
- Perry GLW, Lee F (2019) How does temporal variation in habitat connectivity influence
 metapopulation dynamics? Oikos 128:1277–1286. https://doi.org/10.1111/oik.06052
- Petit S, Burel F (1998) Effects of landscape dynamics on the metapopulation of a ground beetle
 (Coleoptera, Carabidae) in a hedgerow network. Agric Ecosyst Environ 69:243–252.
 https://doi.org/10.1016/S0167-8809(98)00111-X
- Raatikainen KJ, Oldén A, Käyhkö N, et al (2018) Contemporary spatial and environmental factors
 determine vascular plant species richness on highly fragmented meadows in Central
 Finland. Landsc Ecol 33:2169–2187. https://doi.org/10.1007/s10980-018-0731-z
- Rapinel S, Mony C, Lecoq L, et al (2019) Evaluation of Sentinel-2 time-series for mapping
 floodplain grassland plant communities. Remote Sens Environ 223:115–129.
 https://doi.org/10.1016/j.rse.2019.01.018
- Rappaport DI, Tambosi LR, Metzger JP (2015) A landscape triage approach: combining spatial
 and temporal dynamics to prioritize restoration and conservation. J Appl Ecol 52:590–601.
 https://doi.org/10.1111/1365-2664.12405
- 654 Rayfield B (2009) Maintaining Habitat Connectivity for Conservation. University of Toronto
- Rayfield B, Fortin M-J, Fall A (2011) Connectivity for conservation: a framework to classify
 network measures. Ecology 92:847–858. https://doi.org/10.1890/09-2190.1
- Rayfield B, James PMA, Fall A, Fortin M-J (2008) Comparing static versus dynamic protected
 areas in the Québec boreal forest. Biol Conserv 141:438–449.
 https://doi.org/10.1016/j.biocon.2007.10.013
- Reigada C, Schreiber SJ, Altermatt F, Holyoak M (2015) Metapopulation dynamics on ephemeral
 patches. Am Nat 185:183–195. https://doi.org/10.1086/679502
- Ricketts TH (2001) The Matrix Matters: Effective Isolation in Fragmented Landscapes. Am Nat
 158:87–99
- Rothley KD, Rae C (2005) Working backwards to move forwards: Graph-based connectivity
 metrics for reserve network selection. Environ Model Assess 10:107–113.
 https://doi.org/10.1007/s10666-005-4697-2

- Rubio L, Bodin Ö, Brotons L, Saura S (2015) Connectivity conservation priorities for individual
 patches evaluated in the present landscape: how durable and effective are they in the long
 term? Ecography 38:782–791. https://doi.org/10.1111/ecog.00935
- Ruiz L, Parikh N, J. Heintzman L, et al (2014) Dynamic connectivity of temporary wetlands in the
 southern Great Plains. Landsc Ecol 29:. https://doi.org/10.1007/s10980-013-9980-z
- Sahraoui Y, Foltête J-C, Clauzel C (2017) A multi-species approach for assessing the impact of
 land-cover changes on landscape connectivity. Landsc Ecol 32:1819–1835.
 https://doi.org/10.1007/s10980-017-0551-6
- Saura S, Bertzky B, Bastin L, et al (2019) Global trends in protected area connectivity from 2010
 to 2018. Biol Conserv 238:108183. https://doi.org/10.1016/j.biocon.2019.07.028
- Saura S, Estreguil C, Mouton C, Rodríguez-Freire M (2011) Network analysis to assess landscape
 connectivity trends: Application to European forests (1990–2000). Ecol Indic 11:407–416.
 https://doi.org/10.1016/j.ecolind.2010.06.011
- Sprugel DG (1991) Disturbance, equilibrium, and environmental variability: What is 'Natural'
 vegetation in a changing environment? Biol Conserv 58:1–18.
 https://doi.org/10.1016/0006-3207(91)90041-7
- Taylor PD, Fahrig L, Heinen K, et al (2006) Landscape connectivity: a return to the basics. In:
 Connectivity Conservation: maintaining connections for nature. Cambridge University
 Press, Cambridge, pp 29–43
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt.
 Nature 371:65–66. https://doi.org/10.1038/371065a0
- Tulbure MG, Kininmonth S, Broich M (2014) Spatiotemporal dynamics of surface water networks
 across a global biodiversity hotspot—implications for conservation. Environ Res Lett
 9:114012. https://doi.org/10.1088/1748-9326/9/11/114012
- Turner MG, Romme WH, Gardner RH, et al (1993) A revised concept of landscape equilibrium:
 Disturbance and stability on scaled landscapes. Landsc Ecol 8:213–227.
 https://doi.org/10.1007/BF00125352
- Urban D, Keitt T (2001) Landscape Connectivity: A Graph-Theoretic Perspective. Ecology
 82:1205–1218. https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2
- van Ruremonde RHAC van, Kalkhoven JTR (1991) Effects of Woodlot Isolation on the Dispersion
 of Plants with Fleshy Fruits. J Veg Sci 2:377–384. https://doi.org/10.2307/3235930
- Wilson DS (1992) Complex Interactions in Metacommunities, with Implications for Biodiversity
 and Higher Levels of Selection. Ecology 73:1984–2000. https://doi.org/10.2307/1941449
- Wimberly MC (2006) Species Dynamics in Disturbed Landscapes: When does a Shifting Habitat
 Mosaic Enhance Connectivity? Landsc Ecol 21:35–46. https://doi.org/10.1007/s10980 005-7757-8
- Zeigler SL, Fagan WF (2014) Transient windows for connectivity in a changing world. Mov Ecol
 2:1–10. https://doi.org/10.1186/2051-3933-2-1

ACCEPTED MANUSCRIPT

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

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

Type I	Two	А	Before and after the removal of a given element	Global	Assumed	Matisziw and Murray (2009)
Туре І	Two	A	Before and after the removal of a given element	Global	Assumed	Bodin and Saura (2010)
Туре І	Two	A	Before and after the removal of a given element	Global	Assumed	Rubio et al. (2015)
Туре І	Two	А	Spring and late summer	Global	Assumed	Mui et al. (2017)
Туре І	Two	В	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)
Туре І	Two	А	1990 - 2002	Global	Assumed	Rappaport et al. (2015)
Type I	Two	В	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	А	1991 - 2006	Global	Assumed	Liu et al. (2014)
Type I	Two	A	1976 - 2012	Global	Assumed	Liu et al. (2017)

ACCEPTED ³⁰ MANUSCRIPT

Туре І	Two	A	Current and future distributions of species under scenarios of both land use and climate change	Global	Assumed	Mazaris et al. (2013)
Туре І	Two	В	Current and future distributions of species under scenarios of both land use and climate change	Local	Assumed	Mazaris et al. (2013)
Type I	Two	А	1982 - 2012	Global	Assumed	Sahraoui et al. (2017)
Туре І	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.	Horváth et al. (2019)
Туре І	Two	В	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	Тwo	В	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) <i>n</i> edges removals	C	None - (i) 50 nodes and (ii) <i>n</i> edges removal (depending on the threshold distance applied)	Global	Assumed	Urban and Keitt (2001)
Туре І	Multiple: 1 to 30 % (in increments of 1%) node removals in relation to the total number of nodes in the graph	С	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	С	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)	В	No flooding - 100 year average recurrence interval floods	Local	Assumed	Bishop-Taylor et al. (2015)
Туре І	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)
Туре І	Multiple: 3 (mid- 19 th , late-20 th , early 21 st centuries)	C + B	mid-19 th century - early 21 st century	Local	Tested. Result: A loss of connectivity was observed. Time-	Raatikainen et al. (2018)

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

Туре І	Multiple: 5 [0 (initial conditions) and 50, 100, 150, 200 years of 5 alternative protected areas (patches) scenarios]	В	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)

715



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

36

716

717



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

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





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

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



751

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

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

759 Appendix S1 Methods

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

43