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

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Abstract

Context. Landscape connectivity plays a key role in determining the persistence of species inhabiting fragmented habitat patches. In dynamic landscapes, most studies measure connectivity 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.

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

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

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 spatial dispersal of organisms, quantifies temporal changes in spatial connectivity. Based on two 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

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 populations forming a metapopulation (Opdam 1991; Hanski 1994) and species assemblages are 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 and assemblages, because it enables the exchange of individuals among local populations and communities. Dispersal is affected by landscape connectivity, defined as the degree to which the landscape facilitates the movement of individuals among habitat patches (Taylor et al. 2006). However, connectivity varies over time following land cover changes (Taylor et al. 2006; Crooks 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 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 whereas others respond with a time-lag (Ovaskainen and Hanski 2002; Kuussaari et al. 2009). A time-lagged response of species or assemblages to connectivity loss may reflect a relaxation time, resulting in extinction debt (Diamond 1972; Tilman et al. 1994; Kuussaari et al. 2009). Conversely, 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 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. Over the past two decades, studies have focused on the time-lagged responses of biodiversity to connectivity changes, by investigating whether past connectivity explains current species distributions better than current connectivity (for a review of time-lagged response to landscape changes, see Lira et al. 2019). Past and current connectivity were assessed using a spatial 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 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 connectivity have been demonstrated, primarily in plants (van Ruremonde and Kalkhoven 1991; Lindborg and Eriksson 2004; Helm et al. 2006; Naaf and Kolk 2015) but also in mammals, birds, amphibians (Metzger et al. 2009) and invertebrates (Petit and Burel 1998; Bommarco et al. 2014). This approach emphasizes the importance of past connectivity in understanding current biodiversity patterns.

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 current biodiversity patterns would enable effective conservation or restoration actions (Kool et al. 2013; Zeigler and Fagan 2014; Lira et al. 2019). To this end, a range of methods have been attempted to measure the temporal dynamics of connectivity, thereby go beyond the investigation of time-lagged response that rely solely on a quantification of a spatial connectivity index at 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 different time steps into a single index, that account not only for the spatial dispersal of organisms, but also for the probability that organisms disperse among habitat patches over time (hereafter referred to as temporal dispersal). These approaches provide estimates of the temporal dynamics of connectivity that can be related to biodiversity patterns. To our knowledge, there is no existing work yet analysing these approaches, their outputs and their implications for the ecological 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.

2. Main body

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 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 theoretical background, graph theory, applied to landscape ecology. We can divide them into two 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 connectivity, which accounts for both spatial and temporal dispersal (6% of the papers) (see **Table 1** for a detailed synthesis). Graph theory applied to landscape connectivity and its temporal 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 approaches from a conceptual and operational perspective.

2.1 Theoretical background: graph theory

Urban and Keitt (2001) introduced graph theory to landscape ecologists as a modelling framework to assess landscape connectivity. In this framework, the landscape is viewed as a graph composed of a set of nodes corresponding to favourable habitat patches, connected by edges representing potential ecological fluxes (e.g., dispersal) among nodes. The nodes and edges can be weighted by the size or quality of the habitat patches and by the distance between the patches, respectively, to better represent their contribution to connectivity. The edges can be weighted by Euclidean distance, least-cost distance (Adriaensen et al. 2003) or resistance distance (McRae 2006). Euclidean distance is rooted in a binary representation of the landscape (i.e., habitat patches vs uniform matrix), which assumes that organisms disperse along straight lines between two nodes (Forman and Godron 1986). By contrast, the distances resulting from least-cost paths or circuit theory acknowledge that matrix heterogeneity is an important factor in determining the dispersal of organisms (Ricketts 2001). In this framework, a wide range of indices has been developed to 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 entire graph (for reviews, see Galpern et al. 2011; Rayfield et al. 2011; Laita et al. 2011). The 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 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 prospective or retrospective studies. More specifically, the temporal dynamics of connectivity can be predicted or evaluated by simulating virtual changes under different scenarios or by analysing 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 meant only temporal changes in spatial connectivity could be modelled. Recent advances underlined the relevance of spatio-temporal graphs, in which nodes and edges are represented in both space and time in a multiple-layer graph (Dale 2017). This approach combines layers 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 landscape perspective that is useful for the assessment of spatio-temporal connectivity (Rayfield 2009; Fletcher and Fortin 2018).

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.

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.

2.2.1 Two time steps in the time series

The first set of studies (i.e., 17 out of 30 papers) analysed the temporal changes in spatial 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 after the loss or gain in spatial connectivity (**Fig. 3a**). Originally, this approach was used to assess the relative contribution of a given node or edge to the global connectivity, by computing the loss 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 in global connectivity was transposed to a more temporal perspective, for instance to enable 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 indicator" based on the differences in the amount of habitat and global connectivity between t_{before} and t_{after} to enable prioritisation of the landscapes to be protected or restored. These authors 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 land cover changes affect the temporal changes in spatial connectivity, often at global scale (Baudry et al. 2003; Saura et al. 2011, 2019; Liu et al. 2014, 2017; Mazaris et al. 2013; Sahraoui et al. 2017; Mui et al. 2017), and sometimes at the local scale (Mazaris et al. 2013; Mui et al. 2017). For instance, Liu et al. (2017) tested the effect of forest plantation expansion on global spatial connectivity of natural forests. They reported that connectivity loss varied from 55% to 96% 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 forests were planted. Other authors, including Horváth et al. (2019), went further by testing the effect on biodiversity of the variation in local spatial connectivity between 1957 and 2010. In temporary ponds subject to up to 70% of habitat loss, these authors showed that the greater the loss of local connectivity, the greater the loss of invertebrate zooplankton richness over the period concerned. However, they focused on changes in spatial connectivity between two time steps, 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 contrast, through the use of the standard error of the mean and statistical tests, respectively, Bommarco et al. (2014) and Huber et al. (2017) demonstrated significant losses of local connectivity of grasslands before analysing whether a time-lagged response in biodiversity had taken place.

Overall, assessing temporal changes in spatial connectivity based on variations in spatial 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 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. However, additional changes in connectivity may occur between the two time steps, particularly 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 studied ($t_{before} < t_x < t_{after}$) should thus improve the assessment of temporal changes in spatial connectivity.

2.2.2 Multiple time steps t_x in the time series

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**), 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 the curve of global spatial connectivity over successive deletions of nodes or edges (e.g., Urban 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 al. (2014) investigated how the global connectivity of aquatic habitat patches might change in a warmer climate, assumed to lead to aquatic habitat patch loss. They assessed the robustness of the 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 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. 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 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.

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, 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**). 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 appropriate locations for connectivity measures (Foltête et al. 2014; Clauzel et al. 2015; Foltête 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 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 study temporal changes in spatial connectivity as changes in land cover occur. For instance, 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 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 connectivity (1962 and/or 1981) and/or the successive temporal changes in connectivity (1962-1981 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), 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 long time periods (1975-2011, 1945-2000s and 2010-2018), respectively. McIntyre et al. (2018) 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 connectivity values over time which could be crucial for aquatic biodiversity, as shown by Tulbure 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 between time steps in the time series. These differences were assessed by comparing the standard error (Rayfield et al. 2008; Raatikainen et al. 2018) or the 95% confidence interval (Bishop-Taylor et al. 2015) around mean connectivity values. Statistical tests could be also used though already done yet. For instance, Rayfield et al. (2008) analysed temporal changes in global spatial 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 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 demonstrated that global connectivity decreased in most of the scenarios investigated.

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.

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 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 assess the temporal changes in spatial connectivity (Tulbure et al. 2014; Bishop-Taylor et al. 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 global connectivity was subject to high seasonal variability while significantly decreasing over the whole period, suggesting potential consequences for species inhabiting these aquatic habitats. Extending the use of statistical analysis to assess the overall trend of spatial connectivity values at multiple time steps is probably the most promising quantitative and precise approach for the assessment of temporal changes in spatial connectivity. The relationship between time and connectivity can be explored, for instance, through linear, logarithmic, exponential polynomial or power functions. Assessing trends in spatial connectivity at multiple time steps makes it possible to determine not only the significance and the sense of the overall temporal changes in spatial connectivity but also the magnitude of the changes.

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 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 important to reflect the underlying ecological processes as accurately as possible. Besides the sense and magnitude of these temporal changes, their abruptness and their variability can also be assessed (**Fig. 4)**. Trend analysis is a powerful but still underexploited tool to make a finer yet broader 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 the data). Although the effects of the sense and the magnitude of the temporal changes in spatial connectivity still need to be fed by evidence (but see Metzger et al. 2009; Bommarco et al. 2014; 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 also likely drive the dispersal movements of organisms, and hence their response to temporal 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 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.

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

The assessment of the temporal dynamics of landscape connectivity based on a sequence of spatial 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 patches do not only affect spatial dispersal between habitat patches at a given time step, but also 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 forward, by assessing spatio-temporal connectivity using a spatio-temporal landscape graph. Transposed from a landscape perspective, a spatio-temporal graph represents a snapshot of the 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 can be weighted by the spatial distance and the duration of the time series, respectively; but this approach has not yet been explored. Martensen et al. (2017) proposed a similar method, in which spatial and temporal edges are weighted based on the probability of spatio-temporal dispersal (**Fig. 2c**). Each node is weighted by its change over the time series, that is, by habitat patch turnover between t_{before} and t_{after}. Specifically, the node can be either gained (node absent in t_{before} but present in t_{after}), lost (node present in t_{before} but absent in t_{after}) or remain stable (node present in t_{before} and in t_{after}). The weight attributed to the temporal edges between nodes depends on the (possible) simultaneous existence of nodes between the time steps considered (i.e., at t_x, between t_{before} and t_{after}). If the two nodes exist simultaneously at t_x (e.g., if the organism disperses from a node being lost or gained to a stable node between t_{before} and t_{after}), the weight attributed to a temporal edge is 1. If information concerning the simultaneous existence of two nodes at t_x is unknown (e.g., if the organism disperses from a node gained to a node lost between t_{before} and t_{after}, or the opposite), the weight is 0.5. By multiplying the spatial and temporal weight of the edge, the probability of spatio-temporal dispersal between two habitat patches is 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. Martensen et al. (2017) examined the spatio-temporal connectivity before (1990) and after (2001) a hypothesised change in connectivity in a forest landscape. They compared the global connectivity of forest patches obtained from the only-spatial approach based on snapshots of the landscape at the two time steps studied, with those obtained from the spatio-temporal approach based on a 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-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 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 loss of habitat amount, quality and isolation occurred between t_{before} and t_{after}. The authors also investigated how the ability of three “real” species to expand their range under different climate change scenarios affected underestimation of only-spatial connectivity. They found that the difference between future (2030) only-spatial connectivity and the spatio-temporal connectivity measured over the time series [from the present (1970-2018) to future (2030)] declined in species that will probably expand their range, and vice versa. These studies emphasise the need to include the consequences of changes in habitat patches in the ability of an organism to reach habitat patches between two time steps to quantify the "real" (i.e., spatio-temporal) connectivity and its potential consequences for biodiversity.

Overall, the inclusion of both the spatial and temporal components of the dispersal processes 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, which probably justifies the trinary weighting of temporal edges and thus a very simplified view of the process of temporal dispersal. Including multiple time steps t_x will pave the way for possible improvements to accurately fit the dispersal process of organisms, such as the (i) time and the period (e.g., linked to the state of habitat patches) required to disperse among habitat patches and (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 spatio-temporal model of connectivity, by weighting the probability of temporal dispersal between 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 of individuals) but also the probability of species with low dispersal ability to disperse over time 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 it possible to account for the most suitable or required dispersal periods for the organism concerned. Further, the potential legacy effects exerted by connectivity on current biodiversity patterns need to be explicitly accounted for to reach a holistic understanding of how spatio-temporal connectivity 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 time-lag curves (i.e., the degree to which species respond to connectivity at different time steps of the time series studied) in the spatio-temporal connectivity approach.

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 connectivity, it is still not clear if the two main approaches reflect the same ecological processes 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 at multiple time steps, but not between these time steps. Nonetheless, considering the temporal changes in spatial connectivity is one step forward in our understanding of the persistence of (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 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 (meta)-communities were overlooked until the recent works of Perry and Lee (2019) and de Santana et al. (2015). In dynamic landscapes, habitat patch turnover may outweigh the relationships between spatial connectivity and species occupancy, even if the spatial connectivity shapes colonisation processes (Biedermann 2004; Hodgson et al. 2009). Therefore, like habitat loss (Keymer et al. 2000), spatial connectivity should be at least as important as its patterns of temporal changes – if not more so – in determining current biodiversity patterns. But patch turnover also provides spatio-temporal connectivity among patches, thereby allowing individuals to disperse among ephemeral patches over time, even though the patches are spatially isolated at any single time step (Keymer et al. 2000; Matlack and Monde 2004; Wimberly 2006). Omitting the spatio-temporal connectivity may therefore not only lead to the absence of apparent connectivity effects, 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, spatio-temporal 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.

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.

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 thanks to the recent development of powerful tools to (i) rapidly and accurately digitise past land cover maps, such as the HistMapR free package (Auffret et al. 2017) and (ii) obtain accurate data at a frequent time resolution to digitise current land cover maps thanks to the recent advances in remote sensing methods, accessible at low cost, coupled with efficient machine-learning algorithms (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 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 overcoming these constraints.

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-making tools for land-use planners. The difficulty in disentangling the underlying components of the temporal changes in spatial connectivity can also hamper the choice of actions to be 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 toward a realistic and feasible indicator for setting conservation and restoration priorities. We believe that - at present - the joint use of the two approaches would allow more precautionary management of connectivity and its impacts on biodiversity. This combination of approaches could especially help prioritize specific areas to be protected or to be used to implement and test connectivity conservation or restoration measures in a dynamic perspective (i.e., “mobile” protected areas, the locations of which change over time; Bull et al. 2013) to maintain, restore and protect biodiversity in a changing world.

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Availability of data and material (data transparency)

All data analysed during this study are included in this published

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Not relevant

Authors' contributions

Conceived the ideas and designed methodology - LU, AA, CM, AE. Analysed and interpreted the data - LU. Prepared all figures, table, appendix - LU. Led the writing of the manuscript - LU. Contributed critically to drafting and revising the manuscript - LU, AA, CM, JCF, AE. Final approval for publication - LU, AA, CM, JCF, AE.

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

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**
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.	Horváth 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-19th, late-20th, early 21st centuries)	C + B	mid-19th century - early 21st 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.	
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)

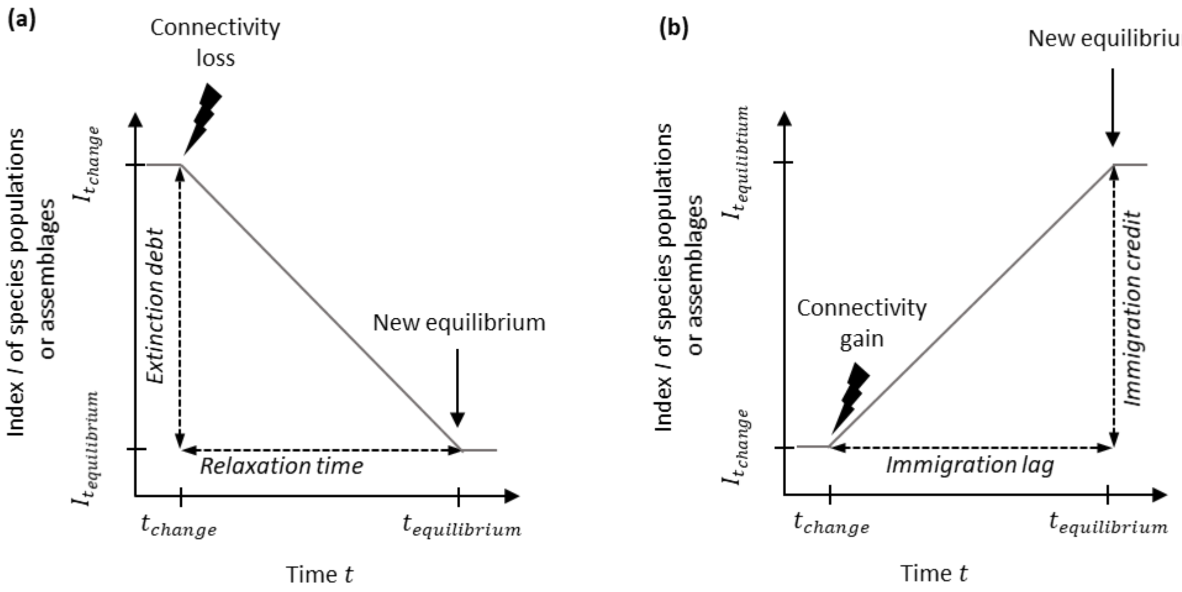

Fig. 1 Illustrations of time-lagged responses and their effects on species populations or assemblages following a **(a)** loss or **(b)** gain in landscape connectivity. t_{change} is the time step at which connectivity changed (either loss or gain) and for which no response of species (either extinction 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).

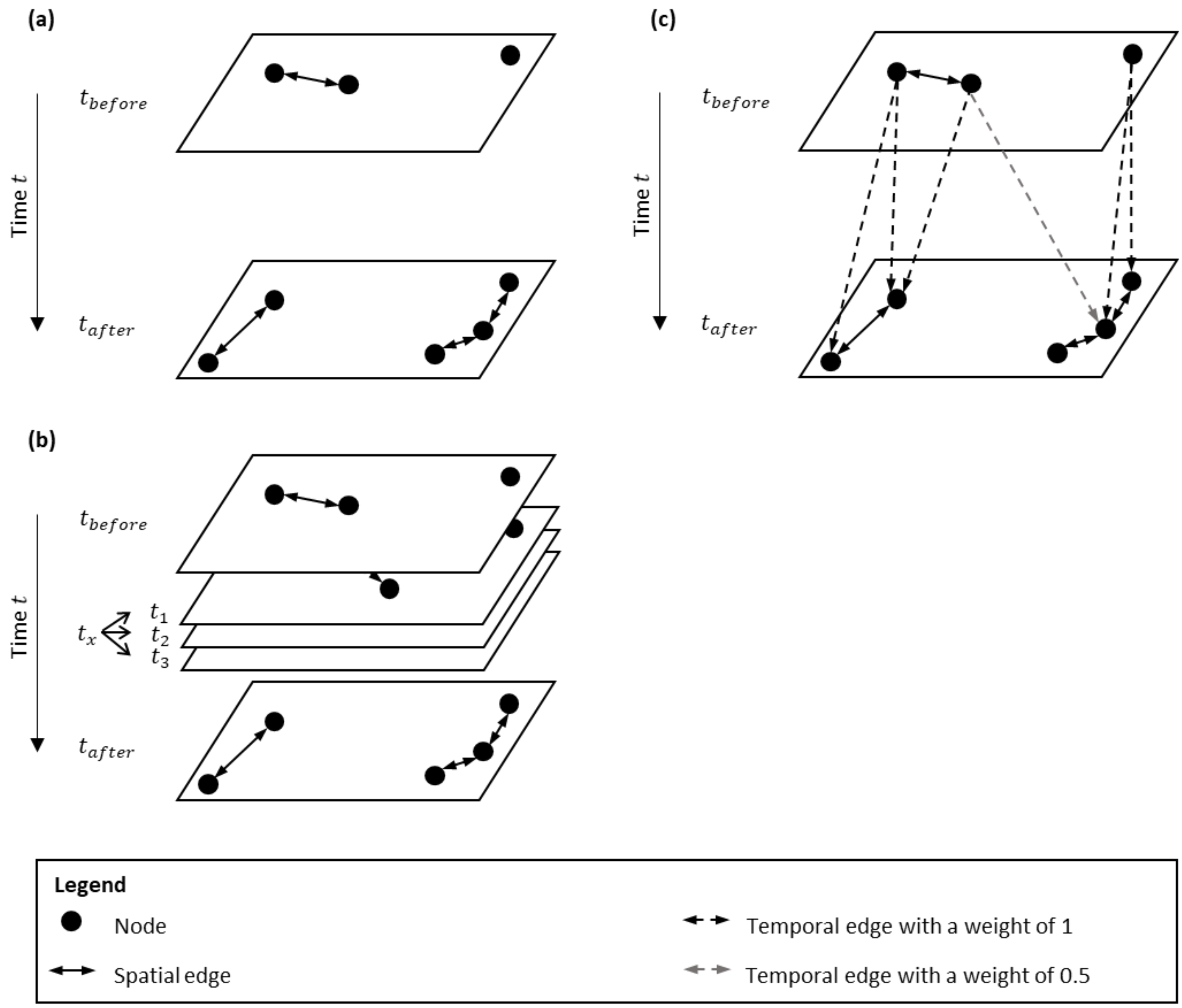

Fig. 2 The temporal dynamics of landscape connectivity can be assessed from spatial landscape graphs (left) either for **(a)** two time steps of the time series [i.e., before (t_{before}), and after (t_{after})] the change in connectivity or **(b)** multiple time steps t_x ($t_{before} < t_x < t_{after}$)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

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 simultanoustly 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).

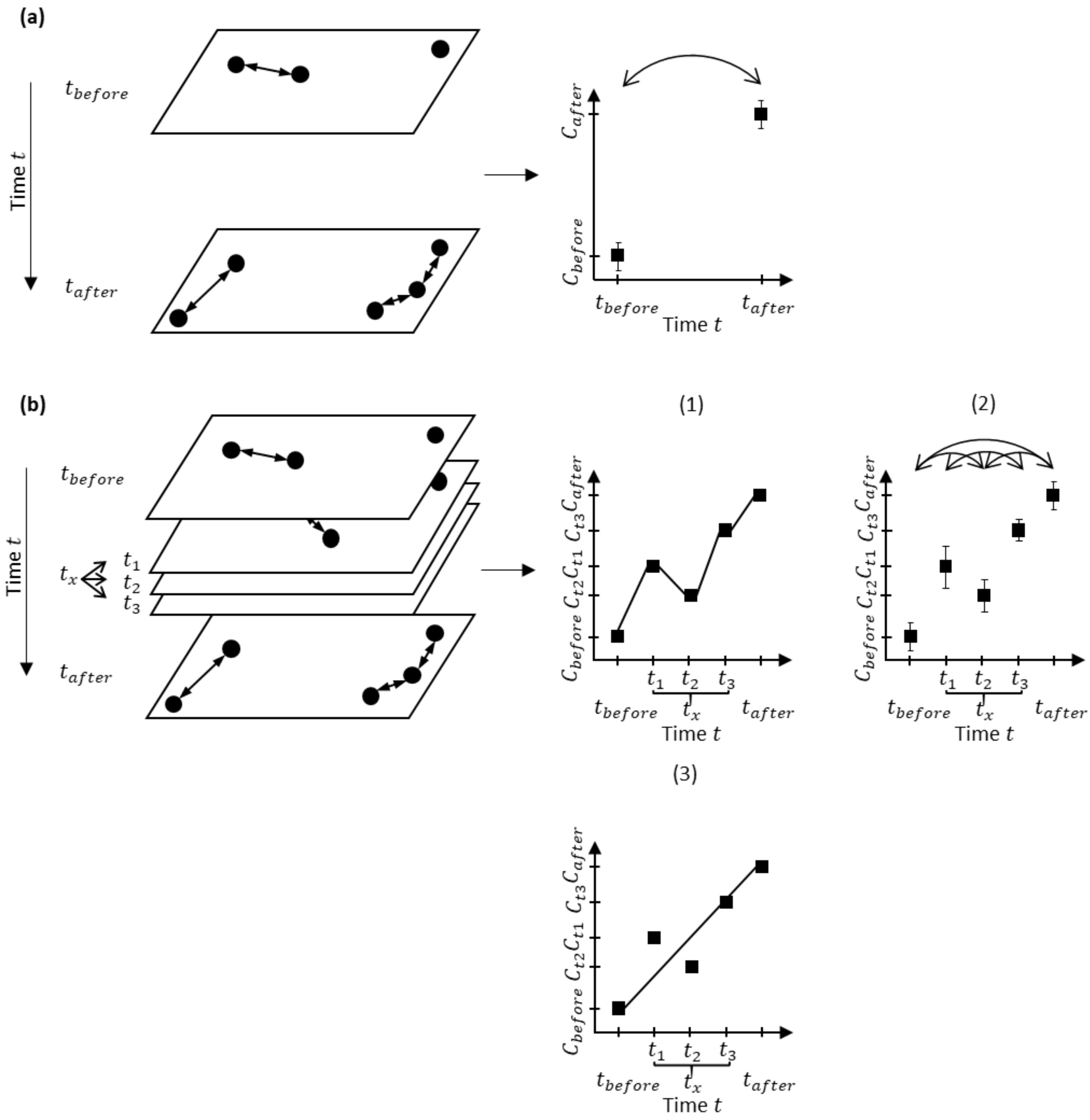

Fig. 3 Overview of possible approaches to assess the temporal changes in spatial connectivity from the comparison of multiple spatial connectivity indices, calculated independently for different time steps in the time series. Such temporal changes can be assessed with **(a)** two time steps in the time 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 analysis.

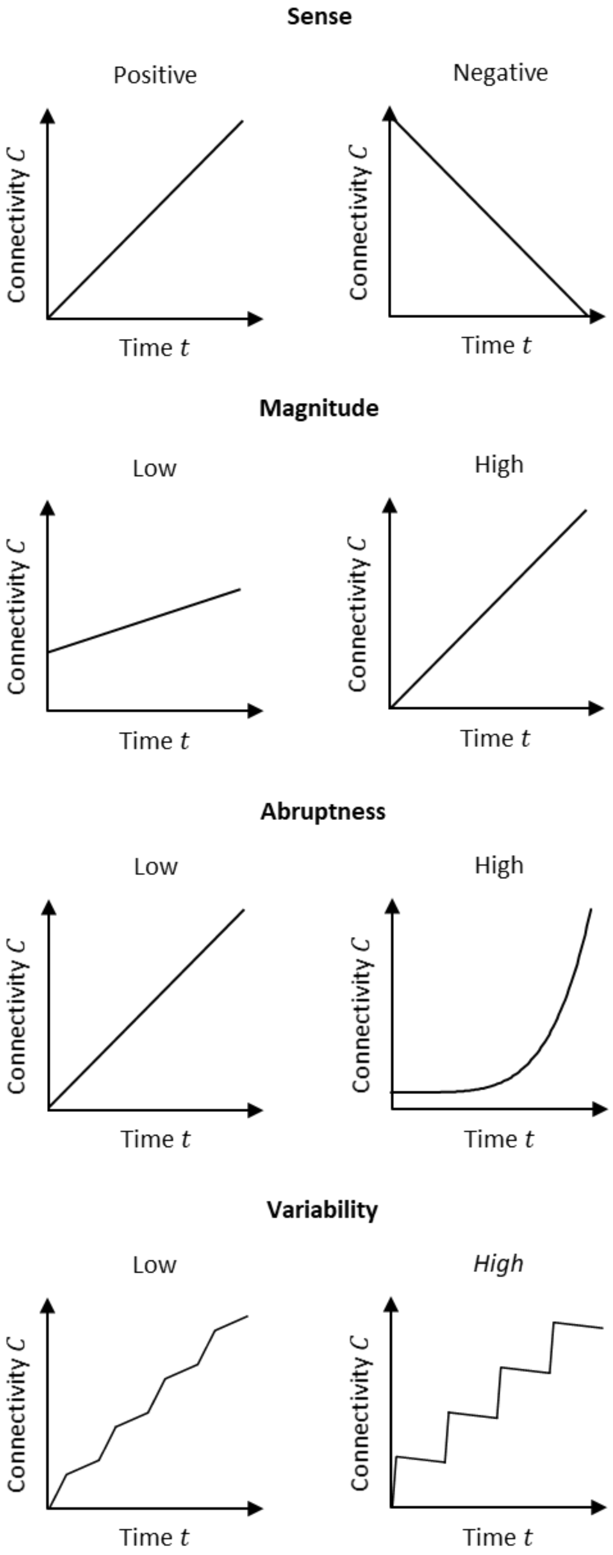

Fig. 4 Overview of the different components of the temporal changes in spatial connectivity that could be provided by statistical modelling of the relationship between time and connectivity (trend analysis). Indicators derived from statistical analysis could infer the sense (i.e., positive or negative

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.

Appendix S1 Methods

We reviewed articles to identify the currently existing methods that aim to assess the temporal dynamics of landscape connectivity. We interrogated Web of Science and Google Scholar with the following keywords: “landscape connect*”, “temporal”, “time”, “dynamics”, “changes” and “variability” to compiled peer-reviewed papers (excluding review papers) that were published up until April 2020. On the basis of the titles and abstracts, we focused on papers which reserved the 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 use for estimating the temporal dynamics of landscape connectivity. We supplemented the few 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; Bishop-Taylor et al. 2018b). Overall, we identified a total of 32 studies.