

Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes

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Summary

1. Landscape heterogeneity and habitat connectivity affect species movements, playing an important role in determining the likelihood of species persistence. However, landscape connectivity is usually evaluated using static snap-shots, which do not account for the sequential interactions among habitat patches through time.

2. We developed a network-based model of landscape dynamics, and corresponding connectivity metrics, to account for the reachable habitat across space and time. We illustrate the behaviour of these metrics, using fragmented forested landscapes in the Atlantic Forest of Brazil. We parametrized the models using the dispersal capacities of selected bird and small mammal species.

3. We found that when considering spatio-temporal links, connectivity is estimated to be on average 30% higher (with a maximum of 150% higher) than what is estimated from purely spatial models. This higher degree of spatio-temporal connectivity arises due to connections through temporal stepping-stone patches that appear (habitat gain) and disappear (habitat loss) over time. Species with short dispersal distances (<1000 m) particularly benefited from the spatio-temporal connections. The contribution of spatio-temporal connectivity to habitat reachability increased with higher habitat loss rates. Moreover, it depended on the amount of habitat in the landscape, being higher at intermediate habitat amounts (~30%).

4. We showed that accounting for spatio-temporal connectivity is critical for understanding ecological patterns and processes in dynamic landscapes, and that a series of purely spatial connectivity metrics underestimates the actual connectivity patterns across time. The proposed spatio-temporal connectivity approach and metrics can be applied to evaluate the effective connectivity patterns and trends in a variety of dynamic landscapes, avoiding the potential overestimates of population isolation and extinction probabilities that may result from widely used purely spatial connectivity models.

Key-words: biodiversity conservation, connectivity metrics, ecological networks, graph theory, habitat amount and configuration, landscape network dynamics, network theory, spatial dynamics, species dispersal ability, stepping-stones

Introduction

Landscape connectivity, i.e. the degree to which landscape heterogeneity affects organism's dispersal, directly influences species movement and therefore modulates gene flow (Coulon *et al.* 2004), as well as the persistence of populations, communities and ecosystems (Mitchell, Bennett & Gonzalez 2013). Hence, connectivity measurements have received great scientific attention, and a broad array of methods and approaches have been used to support its evaluation (Rayfield, Fortin & Fall 2011). However, the influences of landscape connectivity on ecological processes and subsequent patterns are generally evaluated using only static snap-shots (Moilanen & Hanski 2001; Kindlmann & Burel 2008; Claudino, Gomes & Campos 2015), which do not capture temporal interactions among habitat patches that occur in many rapidly changing landscapes (Hanski 2011).

One of the most promising and integrative approaches for evaluating landscape connectivity is the development and application of methods based on network (graph) theory (Urban *et al.* 2009; Dale & Fortin 2010; Blonder *et al.* 2012). Under this framework, habitat patches are represented as nodes, and their potential direct connections as links (Urban & Keitt 2001), which are parametrized based on species dispersal capacities. Network theory has been suggested as a good practical tool to assess connectivity, because it is more informative than simple landscape metrics, yet less demanding in terms of biological data than individual-based models that require movement information (Bodin & Norberg 2007; Fall *et al.* 2007). However, using network dynamics to capture changes in spatial characteristics over time is a mathematically complex process, such that these methods are poorly developed as a result (Blonder *et al.* 2012). So far, the ecological impacts of changes in landscape connectivity have been determined by comparing spatial connectivity analyses performed independently at multiple points in time (e.g. Metzger *et al.* 2009;

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Saura *et al.* 2011; Bommarco *et al.* 2014), ignoring the effects of temporal interactions among habitat patches and the rates of spatial changes through time (Fig. 1).

Here, we propose a novel spatio-temporal network approach and corresponding metrics for quantifying both spatial and temporal connectivity in an integrated fashion. The proposed approach calculates the amount of habitat that can be reached through both spatial and temporal connections, and provides new metrics that are directly comparable to purely static metrics that have been widely used in previous studies (e.g. Saura & Rubio 2010; Saura, Bodin & Fortin 2014 and citations therein). We illustrate the behaviour of these metrics by evaluating a large number of fragmented forested landscapes in the Brazilian Atlantic Forest. Specifically, we assess their behaviour as a function of habitat amount, rate of habitat change (loss and gain), size of the analysed landscapes, and species dispersal capacities. Finally, we highlight the differences in the amount of estimated connectivity based on spatial versus spatio-temporal connectivity

models. We discuss the potential implications of this novel spatio-temporal connectivity approach towards improving our understanding of the ecological patterns and processes that occur in dynamic landscapes.

Materials and methods

SPATIO-TEMPORAL LANDSCAPE NETWORKS

Using a network approach, landscape dynamics can be characterized through changes in both nodes (patches) and their links. Changes in nodes may include losses of entire patches or of parts of patches (shrinkage), patch enlargement, creation of new patches, or changes in patch habitat quality. Depending on species dispersal abilities, these changes in nodes can also translate into connectivity gains or losses because of the changes in links between patches, including changes in the distances between patches and in the availability of intermediate stepping-stones that facilitate movement between patches. Even without changes in habitat patches (nodes), links can vary because of changes in land use between patches. These changes can facilitate or

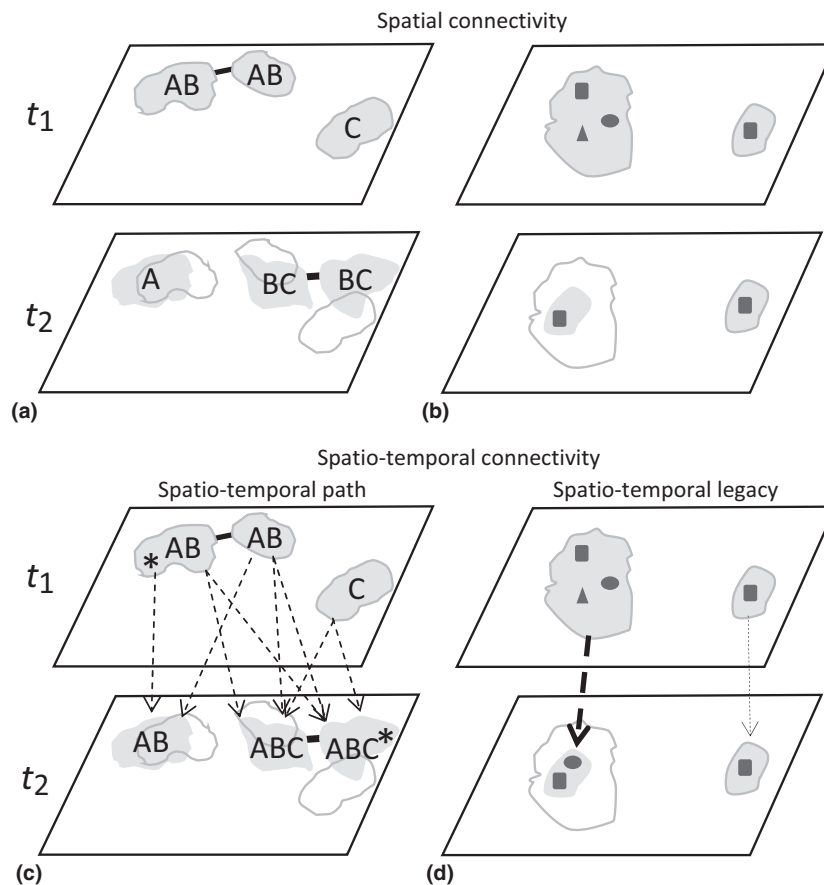


Fig. 1. Spatial (solid lines) and spatio-temporal connectivity (dashed arrows). The grey solid lines in t_2 represent patch locations at t_1 . In (a), the letters represent the populations of a given species with a particular dispersal capacity (AB, C in t_1 and A and BC in t_2). Population AB is connected at t_1 , since both patches are within the species dispersal capacity. The same happens for population BC at t_2 . However, the left-hand fragment and the right-hand fragment are considered isolated when t_1 and t_2 are analysed separately (i.e. without accounting for temporal connections). In (b), although the patches have different sizes and species compositions (different dark grey geometric shapes) at t_1 , the spatial aspects of t_1 do not affect their biological composition at t_2 . When accounting for both spatial and temporal connections, in (c) a given individual (represented by the star) could be in the left fragment at t_1 and in the right fragment at t_2 , but not the other way around (from right to left, temporal directional connection). Additionally, population AB, present in the left and central fragments in t_1 , became isolated in the left patch at t_2 , but is mixed with population C in the central and right patches at t_2 , as represented by ABC. In (d), the large patch in t_1 could provide the small patch in t_2 with more species than an already small patch in t_1 could, as represented by the different width of the dashed arrow and by the different dark grey geometric shapes.

impede movement across the matrix. Links can also vary as a function of seasonal changes, such as floods and droughts, which can temporally connect and disconnect water bodies.

Spatio-temporal connectivity is composed of two features: (i) the spatio-temporal paths, i.e. a sequence of links that can be used to move between two nodes in a network, and (ii) the spatio-temporal legacy (Fig. 1). As spatio-temporal legacy has been widely discussed (see reviews in Kuussaari *et al.* 2009; Hylander & Ehrlén 2013), our novel method aims to characterize and quantify the spatio-temporal paths, which require the joint assessment of spatial and temporal links among patches. As such, a spatio-temporal path across a network represents the possibility of an individual moving from a given habitat node at time t_1 to a different habitat node at a later time t_2 (see acronyms and definitions in Table 1). Two nodes in the network can be connected indirectly (i.e. through a path comprising several links by passing through other intermediate stepping-stone nodes in between) or directly (i.e. through a path consisting of a single link that connects the two nodes directly without using any other intermediate node). From a biological perspective, spatio-temporal paths can be used to calculate the probability that an individual will persist from t_1 to t_2 in a dynamic landscape, particularly when the patch that holds the individual in t_1 does not exist in t_2 (due to habitat loss). In addition, spatio-temporal paths can be used to calculate the probability of a particular individual reaching a given location in t_2 from t_1 , and thus allow for individual and gene flow, enabling connectivity between populations.

MODELLING MOVEMENT IN DYNAMIC LANDSCAPES

Given two dates (t_1 and t_2), all patches in a landscape can be classified into one of the following types:

Stable: habitat in t_1 and in t_2 .

Loss: habitat in t_1 but not in t_2 .

Gain: not habitat in t_1 but habitat in t_2 .

We assume that no more than one type of habitat change occurs between t_1 and t_2 . In other words, the landscape data are measured frequently enough to avoid back-and-forth changes (e.g. habitat loss and gain) for a location within the same time step, yet at a temporal resolution long enough to capture changes between time steps.

We then create a graph representation of the landscape (a network model) in which nodes (patches) are classified in one of these three types and the links directly connecting these patches are defined as described below. We then use network analysis to determine which paths

(comprising one or multiple links) are available for movement through the spatio-temporal graph, as quantified through the spatio-temporal Probability of Connectivity metric (see next section). We are particularly interested in finding the successful spatio-temporal paths, i.e. those paths that allow individuals of a given species to move from a location with habitat at t_1 to a location with habitat at t_2 . For two patches to be considered connected habitat over space and time, a successful spatio-temporal path across the network must exist between the patches, which means that the starting node of the path in t_1 should be of type Stable or Loss and the final node of the path in t_2 should be of type Stable or Gain.

In the proposed graph representation, a link from node i to node j is considered possible from a temporal perspective (value of 1 in Table 2) when i and j simultaneously exist in the landscape at some time t_x ; this is the case for movement from Loss to Stable, or from Gain to Stable. A movement from Loss to Gain or from Gain to Loss may or may not be possible, depending on when the losses and gains occur for the different patches, i.e. they may exist or not simultaneously at some time t_x . For this reason, these movement types are given a likelihood value of 0.5, although any value between 0 and 1 may be given according to particular cases. Additionally, the links can be of two different types (Table 2):

Essential link is a link that, alone, can be used by an individual of a given species to move from a patch with habitat at t_1 (node of type Loss or Stable) to another patch with habitat at t_2 (node of type Stable or Gain). This link is enough to ensure the potential survival of the individual. In addition, any path needs to contain at least one essential link to be successful in the spatio-temporal model, although a successful path may also comprise multiple links including non-essential links, as described below.

Auxiliary link is a link in the graph that does not transport an individual from a location that has habitat at t_1 to a location that has habitat at t_2 (i.e. it is not an essential link as defined above). Therefore, an auxiliary link is not able to ensure by itself the movement and potential survival of the individual through time. However, the concatenation of several consecutive links through a path in the network, including one or more auxiliary links, may allow an individual to indirectly (using at least one intermediate stepping stone patch) move from a location with suitable habitat at t_1 to a location with suitable habitat at t_2 , potentially being able, by doing so, to reach more habitat resources than by using essential links only. There are two types of these auxiliary links. In the first type, an individual makes a first movement in time t_x ($t_1 \leq t_x \leq t_2$) to a Loss patch (auxiliary link) that still has suitable habitat at t_x but

Table 1. List of variables and keyword definitions

Variables/keywords	Type	Description
t_1, t_2, t_x, t_y	Points in time	Initial, final and intermediate points of the time step ($t_1 < t_x < t_y < t_2$)
Essential link	Link type	A link that alone can be used by an individual to move from a patch with habitat at t_1 (node of type Loss or Stable) to another patch with habitat at t_2 (node of type Stable or Gain)
Auxiliary link	Link type	A link that alone does not transport an individual from a location that has habitat at t_1 to a location that has habitat at t_2 . Therefore, an auxiliary link is not able by itself to ensure the movement and potential survival of the individual through time, although it may allow to reach more habitat resources that by using essential links only
Direct path	Movement type	Consists of a single link (of type essential) from a patch with habitat at t_1 (node of type Loss or Stable) to another patch with habitat at t_2 (node of type Stable or Gain), without using intermediate stepping-stone patches
Indirect or stepping-stone path	Movement type	Comprises multiple links from a patch with habitat at t_1 to another patch with habitat at t_2 going through one or several intermediate stepping-stone patches. It needs to have at least one essential link among the links used, and could have many essential and/or auxiliary links
i, j, k	Nodes	Any given node

Table 2. Temporal links between source (t_1) and destination (t_2) nodes, not considering the spatial constraints

Type of source node: individual location at t_1 for the essential links or at t_x ($t_1 < t_x < t_2$) for the auxiliary links	Type of destination node: individual location after t_1					
	Essential link (individual location in t_2)			Auxiliary link (individual location in t_y , $t_x < t_y < t_2$)		
	Stable	Loss	Gain	Stable	Loss	Gain
Stable	1	0	1	n/a	1	n/a
Loss	1	0	0.5	n/a	1	n/a
Gain	0	0	0	1	0.5	1

Temporal links are directional (asymmetric) from t_1 to t_2 (source to destination). A value of 1 indicates that such link is possible at some moment within the analyzed period. A value of 0 indicates that it is not possible from t_1 to t_2 . A value of 0.5 indicates that the link is possible given some assumptions on the co-occurrence of nodes within the time interval. n/a indicates that these cases are not applicable for the auxiliary links.

will have no suitable habitat at t_2 . In this case, the individual will need to use some other link to move somewhere else after t_x but before t_2 . In the second type an individual makes a movement in time t_x ($t_1 \leq t_x \leq t_2$) from a Gain patch (auxiliary link) that has habitat at t_x but had no habitat at t_1 . In this case, the individual had to be located in some other patch with habitat at t_1 , and hence the individual must have previously used some other link in the graph to get to the patch where it is located in t_x .

Successful paths must include at least one essential link, but they can include other essential or auxiliary links as well. In other words, a successful path can be (i) a direct path consisting of a single link (not passing through other intermediate stepping-stone patches), meaning that this link is necessarily an essential link, or (ii) an indirect path consisting of any combination of multiple auxiliary or essential links, as long as at least one of them is an essential link. Indirect successful paths will hence use one or several intermediate stepping-stone patches in the movement between the source (t_1) and destination (t_2) patches. Examples of indirect successful paths, i.e. including multiple links and one or more stepping-stone patches along the movement, are:

- (i) A concatenation of links all connecting different Stable patches (essential links). Such concatenation is not strictly necessary for individual survival given that the individual is already at t_1 in a location with habitat that will remain so at t_2 (Stable patch). However, the model accounts for the entire set of nodes and all the amount of habitat resources that can be reached by moving through the network, even if the probability is lower for the traversal of longer distances.
- (ii) A link from a Loss to a Stable patch, followed by a link from a Stable to a Gain patch, and by one or several links between different Gain patches. Similarly to the previous case, an individual may be already able to persist, using just the first link (which is an essential link as defined above). However, this does not exclude the possibility that it can also colonize other patches that are too far apart to be reached directly from the initial location but are connected through other intermediate stepping-stone nodes across the network. This path contains an example of the second type of auxiliary link as described above.
- (iii) One or several links between different Loss nodes followed by a link from a Loss to a Gain node. The Gain node may not be reached directly from the first Loss node of the sequence because

they are too far apart from each other given the dispersal abilities of the focal species. One or several other Loss nodes can, however, act as stepping stones allowing the final arrival at the Gain node after concatenating several movement steps. This path contains an example of the first type of auxiliary link described above.

In this way, the network model accounts for all possibilities of spatio-temporal connectivity between patches, either directly or indirectly through one or more stepping-stone patches (Fig. 2), while also acknowledging that not all possible link combinations (paths) will lead to a successful movement that allows for individual potential persistence (e.g. any path ending in a Loss patch will not be successful even if it includes one or more essential links in previous movement steps).

In addition, the possibility of movement in a temporal perspective (e.g. from Loss to Stable) does not mean that such movement is possible from a spatial perspective. If two nodes are too far apart from each other based on the dispersal abilities of the focal species, or are separated by a hostile land cover that acts as a barrier, the movement between the nodes will not be possible even if the patches exist at the same time. Hence, both the spatial and temporal constraints (possibilities) for movement are considered and integrated into the connectivity model; the spatial probabilities for movement are multiplied by the temporal probability for movement (0, 0.5 or 1, Table 2) to obtain the final spatio-temporal links and their associated paths and movement probabilities. The spatial probabilities of movement are obtained from the combination of the species dispersal abilities with the distance between patches. This distance between patches could be of any kind: for example Euclidean distance, or a more complex cost-weighted distance accounting for matrix heterogeneity and resistance. In the latter case, if changes in the landscape matrix occur at t_x , it would translate into variations in the effective distances from t_1 to t_2 . If no information about when those changes occurred within the period between t_1 and t_2 is available, such changes may be accounted for by considering an effective distance equal to the average of that in t_1 and t_2 . More precise information about t_x may allow adjusting the considered effective distance to a value closer to that in t_1 or t_2 depending on whether the changes occurred earlier or later within the time step. Note that the spatial probabilities for movement, as given by dispersal kernels (e.g. negative exponential functions), will decrease when larger Euclidean or effective distances need to be traversed (either because of a long direct movement or of the combination of several stepping-stone movements) to reach a node j from a node i .

These rules form a spatio-temporal model that corresponds to a directed network with asymmetric links, since even if movement from i to j may be possible, it does not imply that movement from j to i is also possible.

METRICS OF SPATIO-TEMPORAL HABITAT REACHABILITY

Given our network model of spatio-temporal connectivity, we now generalize and adapt two existing habitat availability (habitat reachability) metrics, namely the Probability of Connectivity (PCs) and Equivalent Connectivity (ECs) (Saura & Rubio 2010; Saura, Bodin & Fortin 2014), to account for both the spatial and temporal dimensions. Henceforth, we use PCs_{st} and ECs_{st} to refer to our new spatio-temporal metrics, and PCs and ECs for the standard spatial-only metrics; note that the values of the spatio-temporal metrics here proposed are directly comparable with those obtained from the purely static analyses (Table 3).

These metrics express connectivity as the amount of reachable habitat resources in a landscape. They account for both the habitat

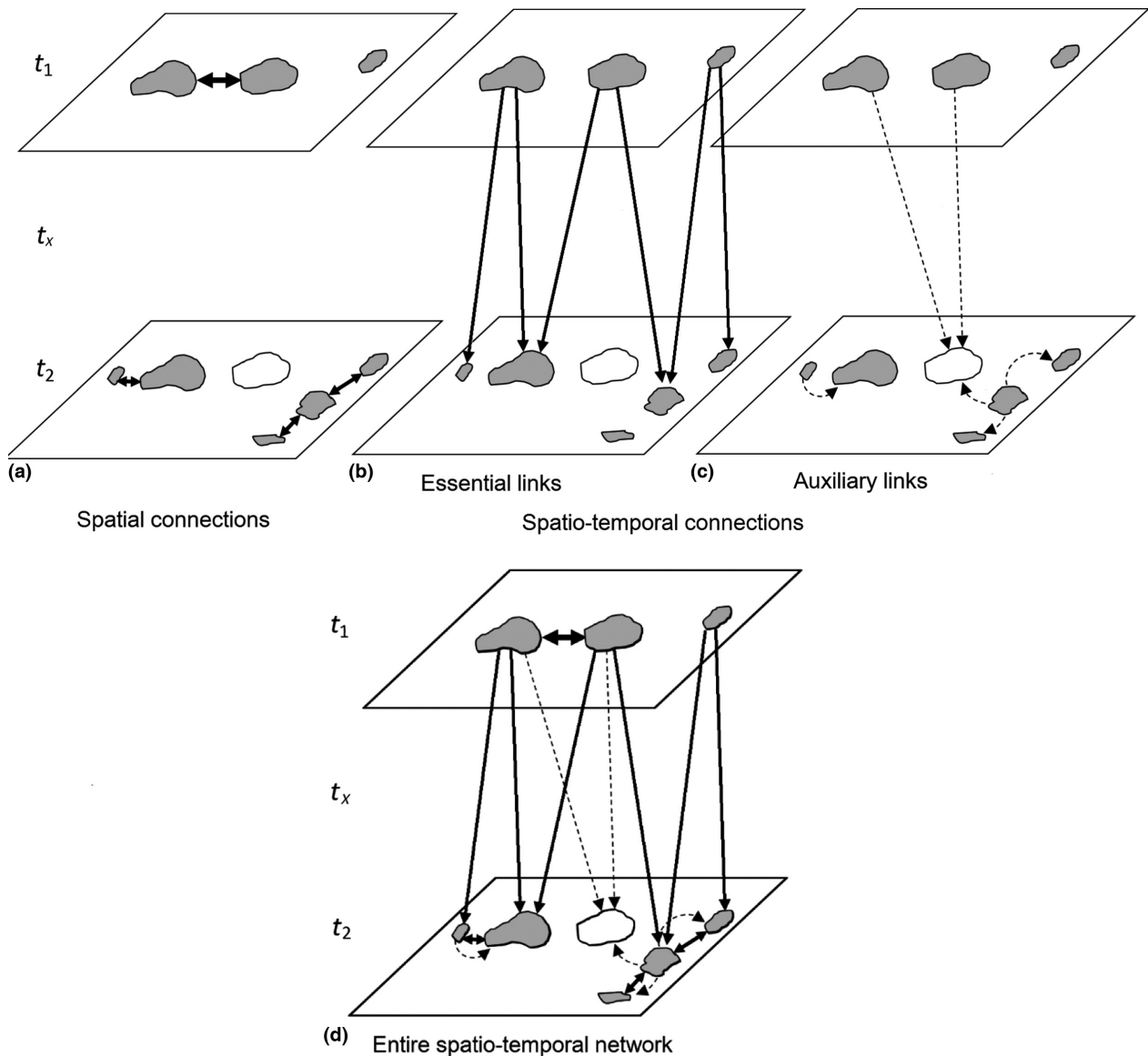


Fig. 2. Spatial (bidirectional) and spatio-temporal (directional) links. (a) Purely spatial connections, (b) Essential links in the spatio-temporal context, (c) Auxiliary links, representing their role in spatio-temporal stepping-stones paths, and (d) the entire spatio-temporal network. In the spatio-temporal context, essential links are represented as solid arrows and auxiliary links as dashed ones. The hollow polygons at t_2 represent the polygons that were lost; therefore, connections to hollow polygons represent connections at t_x .

resources (e.g. habitat area) that can be reached within the patches (intrapatch connectivity) and for the habitat resources that can be reached by moving to other patches through the links in the network (interpatch connectivity), either directly or indirectly. Intrapatch spatio-temporal connectivity occurs when individuals can persist by staying in the same Stable patch from t_1 to t_2 . Interpatch spatio-temporal connectivity occurs when a successful movement between patches happens, i.e. when an individual moves from a Stable or Loss node in t_1 to a different Stable or Gain node in t_2 .

Given two point locations (source i and destination j) randomly selected within the landscape (i in t_1 and j in t_2), $PCst$ is defined as the probability that i and j fall into habitat areas that are spatio-temporally connected in such a way that it is possible for an individual located in i at t_1 to move to j at t_2 . $PCst$ is hence the sum of the probability corresponding to the intrapatch connectivity (i and j falling within the same habitat patch, and that patch being of type Stable)

and the interpatch connectivity (i and j falling into different but connected habitat patches).

$ECst$ is defined as the amount of resources (e.g. habitat area, nesting spots) of a single Stable habitat patch (existing throughout t_1 to t_2) that would provide the same probability of spatio-temporal connectivity ($PCst$) as the network composed by the multiple Loss, Gain and Stable habitat nodes of the landscape. EC is denoted as Equivalent Connected Area (ECA) if habitat area is used as the attribute of the nodes in the network, as we will do hereafter. $ECAst$ gives the effective area of habitat that individuals would be able to reach in the spatio-temporal network, and is calculated as the square root of the numerator of $PCst$ (Table 3).

In addition, the spatio-temporal connectivity $PCst$ can be divided into three fractions: $PCintrast$, $PCdirectst$ and $PCstepst$, which are here expressed as percentages of $PCst$ (Table 3). Each of these fractions quantifies a different contribution to the spatio-temporal connectivity

Table 3. Metrics description and equations

Metrics	Description	Equation
PC _s PC _{st}	Given two locations (source and destination) randomly selected within the landscape, the Probability of Connectivity (PC) is the probability that these two locations fall into habitat areas that are connected, so that it is possible for an individual to move from source to destination. PC can be partitioned in three fractions that are described below (PC = PC _{intra} + PC _{direct} + PC _{step})	$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j P_{ij}^*}{A_L^2}$
ECA _s ECA _{st}	The Equivalent Connected Area (ECA) is the size of a single patch that provides the same value of the Probability of Connectivity (PC) as the observed habitat pattern in the landscape	$ECA = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j P_{ij}^*}$
PC _{intra} _s PC _{intra} _{st}	The fraction of PC that corresponds to the intrapatch connectivity—i.e. the amount of reachable habitat within Stable patches (for the spatio-temporal case) or within all patches (for the purely spatial case).	$PC_{intra} = \frac{\sum_{i=1}^n a_i^2}{A_L^2}$
PC _{direct} _s PC _{direct} _{st}	The fraction of PC that corresponds to the interpatch connectivity provided by direct paths between patches (without using intermediate stepping-stones)	$PC_{direct} = \frac{\sum_{i=1}^n \sum_{j=1, j \neq i}^n a_i a_j P_{ij}}{A_L^2}$
PC _{steps} _s PC _{steps} _{st}	The fraction of PC that corresponds to the interpatch connectivity provided by indirect connections made possible by intermediate stepping-stone patches between source and destination patches	$PC_{step} = \frac{\sum_{i=1}^n \sum_{j=1, j \neq i}^n a_i a_j (P_{ij}^* - P_{ij})}{A_L^2}$

All metrics can be calculated for a spatial-only model (denoted with the suffix *s*) or for the proposed spatio-temporal model (denoted with the suffix *st*). *n* is the number of habitat patches, *a_i* and *a_j* are the attributes of the patches (here habitat area), *P_{ij}^{*}* is the maximum product probability of the paths between patches *i* and *j* (accounting for both direct and indirect stepping-stone movements), *P_{ij}* is the direct dispersal probability between patches *i* and *j* (without using any intermediate stepping-stone patch), and *A_L* is the maximum landscape attribute (here total landscape area). See Saura & Rubio (2010), and Saura, Bodin & Fortin (2014) for further details.

of the landscape. PC_{intra}_{st} corresponds to the intrapatch connectivity (amount of reachable habitat within Stable patches), PC_{direct}_{st} corresponds to the interpatch connectivity provided by direct paths (i.e. direct spatio-temporal connections) between patches (without using intermediate stepping-stone patches), and PC_{steps}_{st} corresponds to the interpatch connectivity provided by indirect connections made possible by stepping-stone nodes between the source and destination nodes (see Saura, Bodin & Fortin 2014 for details of these fractions for the purely spatial metrics).

To calculate PC_{st}, the three PC_{st} fractions, and ECA_{st} we:

- Account for the essential and auxiliary links, and for the different types of paths, i.e. direct and indirect (Tables 1 and 2), as quantified through the maximum product probability paths (Saura & Pascual-Hortal 2007; Saura & Rubio 2010) in the PC metric (here PC_{st}).
- Define two network nodes for each of the Loss and Gain habitat patches. Two nodes are needed per patch because the Loss and Gain patches may function differently in the spatio-temporal network depending on the cases. In some cases, these patches can be an initial starting point (Loss at *t*₁) or a final destination (Gain at *t*₂) in a path across the network, therefore providing habitat resources for the species that can be used before or after the change in the landscape. In other cases, these patches may only act as a temporary stepping-stone at time *t_x* in a multi-step movement among other patches, i.e. as a node that is not the source nor the destination of a successful movement, but just a connector or movement conduit between other patches further apart.
- Calculate the intrapatch connectivity for the Stable patches, as it is possible that an individual that is in a Stable habitat patch at *t*₁ remains in the same patch until *t*₂.
- Finally combine the potential movements in the temporal dimension with the spatial constraints for movement.

Calculations are performed by combining an R script with a command line version of the Conefor software package (www.conefor.org) adapted to spatio-temporal directed networks (both available as supplementary material, Data S2).

Case study in the Atlantic Forest

To demonstrate the proposed network approach and metrics, and to explore their behaviour in dynamic landscapes with different amounts of habitat and rates of land use change, we used a spatial dataset from a 2.3 million hectare region in the north-east of Brazil. The area was originally covered by Atlantic Forest, one of the most fragmented and species rich biomes of the world (Myers *et al.* 2000). We analysed forest habitat changes between 1990 and 2001 in 200 random sampled landscapes of 25 000, 50 000 and 100 000 ha (see Supplementary Material).

MODEL PARAMETERIZATION

In order to keep our example simple, we used patch size of natural forest in hectares as the node attribute for calculating PC_{st}, PC_s and related metrics. However, users can select any other patch attribute, such as population size, habitat quality, or patch area weighted by habitat quality. Here, we selected five median species dispersal distances: 50, 100, 200, 500 and 1000 m. A negative exponential function of interpatch distance was used to obtain the probability of direct movement between any pair of patches (although other dispersal kernels could be also used in the model). The function was parameterized so that it gave a 0.5 probability of movement (gap crossing) between patches when the patches were separated by an edge-to-edge Euclidean distance equal to the considered median dispersal distance. For the tropical biomes (Moore *et al.* 2008) and the Atlantic Forest in particular, few studies are available for birds and small mammals. Studies that are available suggest that the bulk of species have dispersal capacities below 200 m across gaps, with a few species able to cross gaps of many hundreds of meters (Crouzeilles, Lorini & Grelle 2010).

Therefore, with the selected dispersal distances, we are covering a large range of potential dispersal abilities for species in the region. Nevertheless, to further explore the behaviour of the different metrics for larger dispersers, we also used medians of 2500, 5000, 7500 and 10 000 m for dispersal distances for a subset of the landscapes ($n = 5$). We used Euclidean distances and hence treated the non-forest matrix as homogeneous in order to keep the illustrative case study simple, but resistance surfaces and cost-weighted (effective) distances between patches could also be used.

We also built nine linear univariate models to evaluate the effect of the following landscape characteristics on the PC_{st} fractions: (i) habitat amount in t_1 , (ii) habitat amount in t_2 , (iii) amount of stable habitat, (iv) the net difference in habitat amount, (v) the amount of habitat that was lost, (vi) the amount of habitat that was gained, (vii) the proportion of area that was lost, (viii) the proportion of area that was gained, and (ix) the proportion of the differences between total habitat amount in t_1 and t_2 , based on the amount of habitat in t_1 . Finally, we used the model that was best supported among those outlined above to evaluate how PC_{st} fractions respond to these changes.

Results

Spatio-temporal connectivity (ECA_{st}) is c. 30% higher than spatial-only connectivity in t_2 (ECA_s), reaching close to 150% in some cases (Fig. 3), with a slight influence from species dispersal capacity (Fig. 3b). The additional contribution of spatio-temporal connectivity is not much affected by landscape size, but is slightly lower in smaller landscapes (Data S1). The

increase in ECA_{st} compared to ECA_s t_2 is higher with larger amounts of habitat change (Fig. 3). Farther-dispersing species are less influenced by reductions in habitat amount than shorter dispersers (Fig. 3b). Even landscapes with a stable net habitat (similar gains and losses) show increases in ECA_{st} over ECA_s t_2 of around 10%. The higher value of ECA_{st} over ECA_s t_2 holds even for landscapes that have a net habitat gain of around 5% (Fig. 3b). How much greater ECA_{st} is when compared to ECA_s t_2 depends on habitat amount, with a peak at around 30% of habitat, independent of species dispersal capacity (Fig. 4).

The contribution of PC_{step} and PC_{intra} to total connectivity varies as a function of the three analysed scenarios (the purely spatial scenarios for t_1 and t_2 and the spatio-temporal scenario), whereas PC_{direct} represents around 20% of the total PC in all the three scenarios (Fig. 5). PC_{intra} is lower and PC_{step} higher for t_1 and st , whereas the opposite is true for t_2 (Fig. 5). When considering species dispersal capacities, there is a general trend of increasing PC_{step} fraction associated with increased dispersal capacities for all scenarios (t_1 , t_2 and st , Figs 6 and 7). However, this PC_{step} increment happens for shorter dispersing species in t_1 and st , whereas just for farther dispersers in t_2 (Fig. 6). These results are largely independent of landscape size (Figs S3–S6).

Considering all landscape sizes and dispersal capacities, the best supported models (total models = 45) that were able to explain the variations in the fractions of PC_{st} were the ones that included the proportion of habitat loss (60%, 27 times) and also the amount of habitat lost (31%, 14 times). The PC fractions behaviour, according to the proportion of habitat loss, varies as a function of species dispersal capacity (Fig. 7).

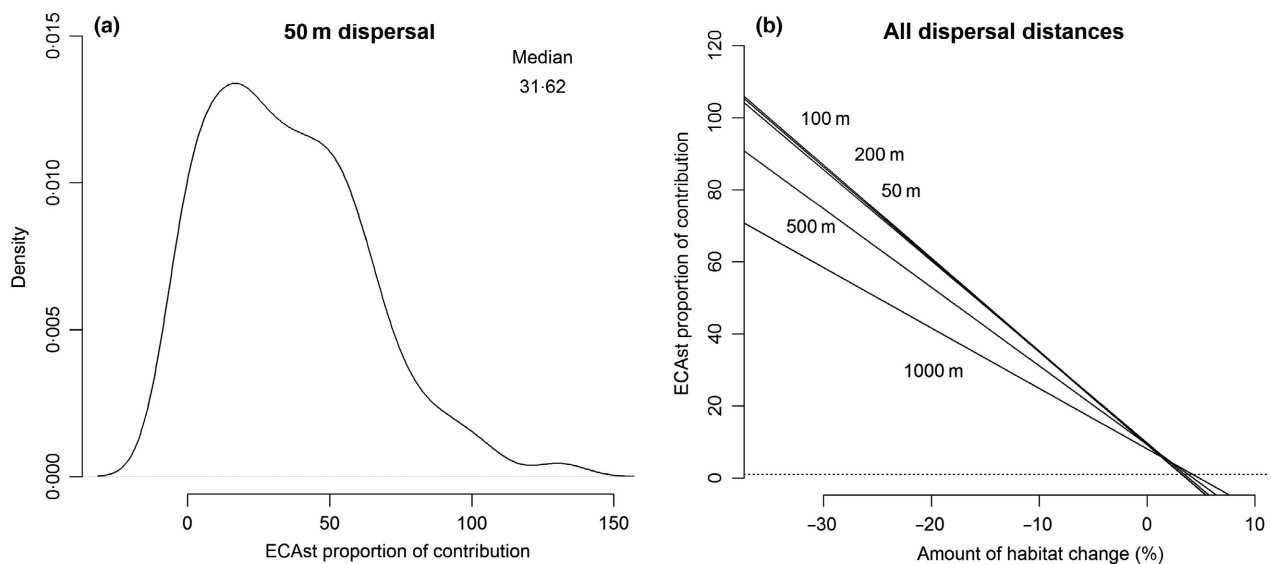


Fig. 3. Contribution of the spatio-temporal connectivity ECA_{st} (Spatio-temporal Equivalent Connected Area, see Table 3) compared to the purely spatial connectivity ECA_s (Spatial Equivalent Connected Area) at t_2 ($100(ECA_{st}/ECA_s t_2) - 100$); (a): density functions of the contribution of the ECA_{st} as a function of ECA_s at t_2 for a median dispersal distance of 50 m. Positive values represent a positive influence of the spatio-temporal connectivity over the purely spatial connectivity in t_2 . Negative/zero values represent cases where either there was no influence of spatio-temporal connectivity, or the increase in the purely spatial connectivity in t_2 was so high that any increase in connectivity caused by the spatio-temporal metrics was surpassed by the purely spatial connectivity at t_2 . (b): The linear models of the percentage of the increment given by ECA_{st} compared to ECA_s at t_2 for all dispersal capacities.

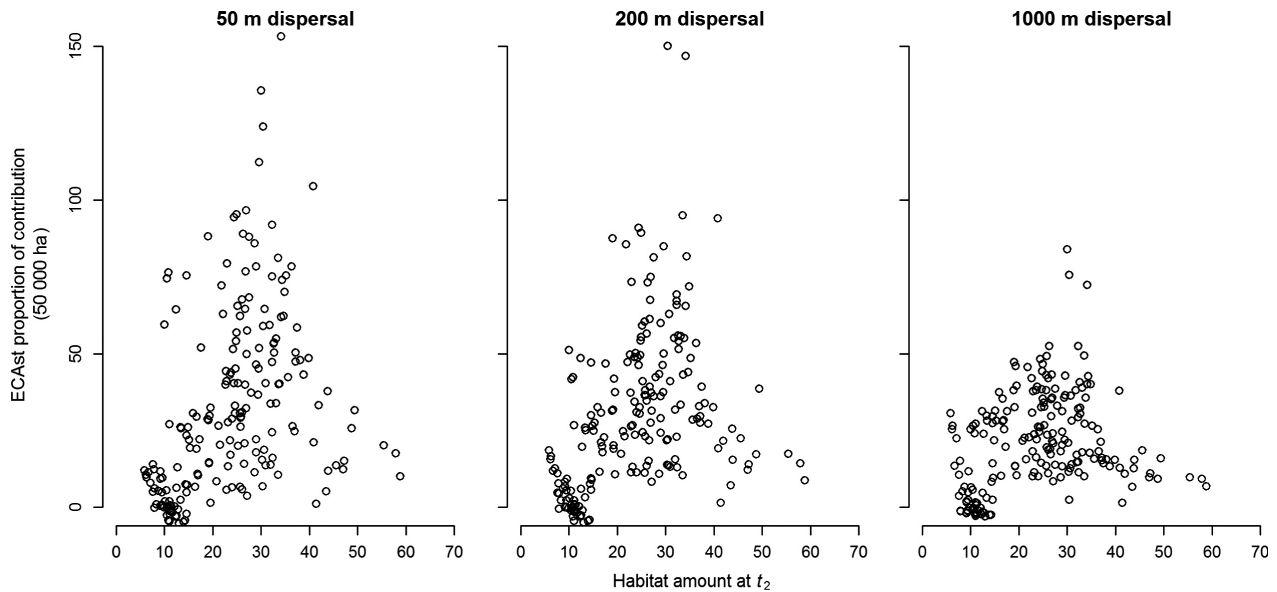


Fig. 4. Contribution of ECA_{st} compared to $ECA_{s t_2}$ ($100(ECA_{st}/ECA_{s t_2}) - 100$) as a function of the amount of habitat in t_2 for three different dispersal distances. See Table 3 for metrics descriptions and calculations.

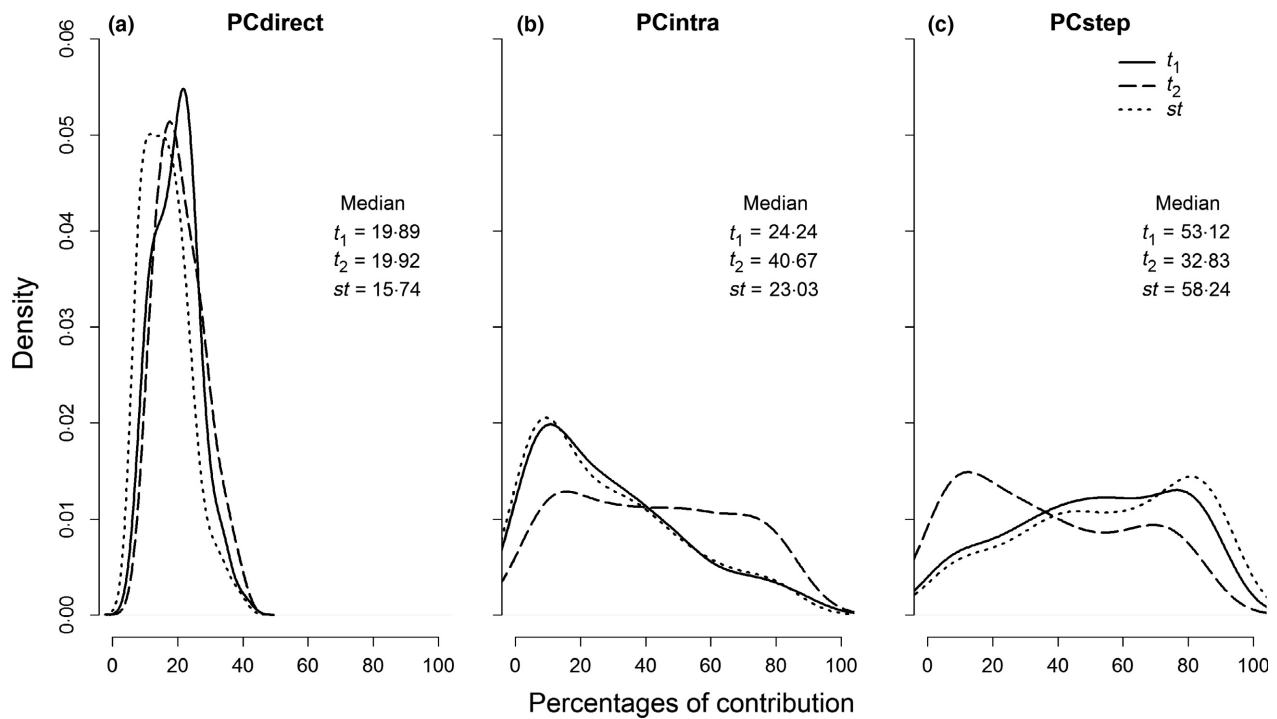


Fig. 5. PC (Probability of Connectivity) fractions for all dispersal capacities. (a) PCdirects in t_1 , t_2 and PCdirectst in the spatio-temporal model; (b) PCintras in t_1 , t_2 and PCintrast; and (c) PCsteps in t_1 , t_2 and PCstepst. See Table 3 and Fig. 2 for metric descriptions and calculations.

For short dispersal species, with low amounts of habitat loss, PCintrast is by far the most important fraction, accounting for around 80% of the PCst, whereas low values are obtained for PCdirectst and PCstepst, although slightly higher for PCdirectst (Fig. 7). However, when the amount of habitat loss increases, the importance of PCintrast drops, and the importance of PCstepst increases, whereas PCdirectst remains stable. For low dispersal species (50 m), at around 20% of habitat

loss, PCstepst started to be more relevant than PCintrast. For species with higher dispersal capacities (1000 m for example), the fractions are somewhat similarly important for low amounts of habitat loss, but PCstepst increases (while PCdirectst and PCintrast decrease) for larger amounts of habitat loss. For these longer dispersing species, PCstepst is larger than PCintrast at already 10% of habitat loss. For species that are able to disperse for even longer distances, such as 2500, 5000

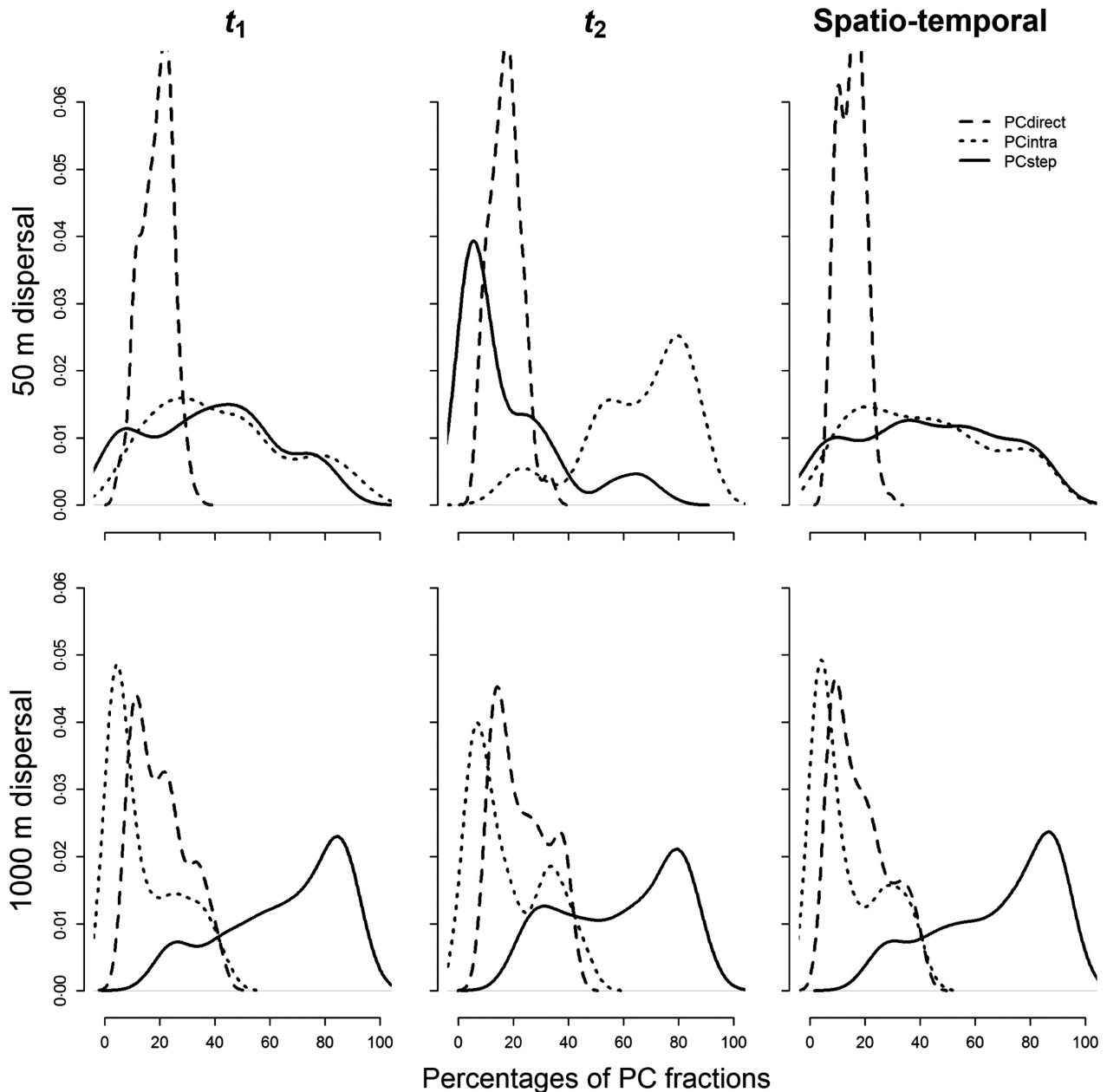


Fig. 6. PC fractions contributions for two different dispersal capacities (50 and 1000 m) in t_1 , t_2 (for the spatial-only PCs) and in the spatio-temporal model (PC_{st}). See Table 3 for metric descriptions and calculations.

or 10 000 m, the importance of PC_{stepst} is reduced, and PC_{directst} increases (Fig. S7).

Discussion

Spatio-temporal connectivity has a positive effect on landscape connectivity for all considered landscape sizes and species dispersal capacities. Increases in connectivity occur primarily through additional spatio-temporal pathways that appear or disappear between time steps (i.e. temporal stepping-stone patches). We showed that measuring connectivity based on purely static spatial metrics substantially underestimates connectivity levels, usually by 30%, but in some cases by nearly

150%. Therefore, not accounting for spatial dynamics could severely overestimate population isolation and extinction probabilities in changing landscapes.

We also demonstrated that accounting for spatio-temporal connectivity is particularly important in landscapes with high levels of habitat change and with net habitat loss, which is common in the tropical regions (Hansen *et al.* 2013). In the tropics, both afforestation, given passive forest regeneration, and deforestation given demands for agricultural expansion, are occurring concomitantly and at high rates (Lambin, Geist & Lepers 2003). These factors ultimately generate a scenario where spatio-temporal patterns are complex, but particularly relevant drivers of ecological processes and patterns. However,

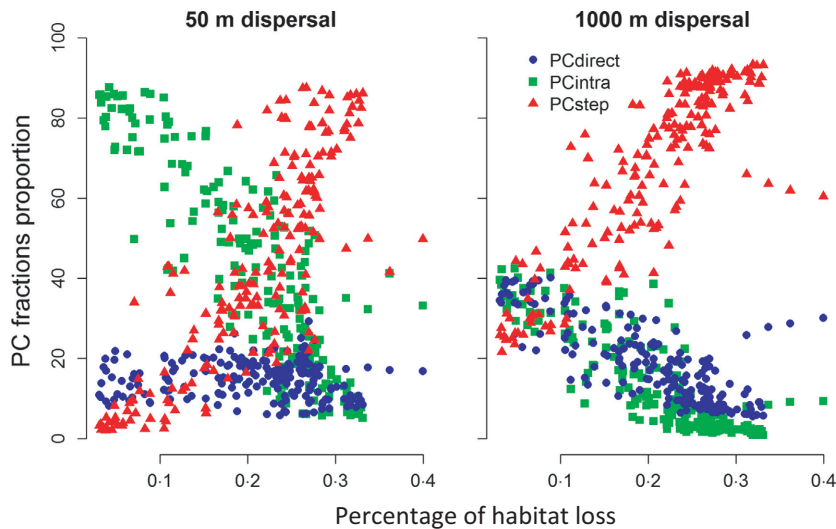


Fig. 7. PCst fractions (blue: PCdirectst, green: PCintrast and red: PCstepst) contribution as a function of the percentage of habitat loss for 50 and 1000 m dispersal distances. See Table 3 for metric descriptions and calculations.

the spatio-temporal legacy is commonly investigated in extinction debt studies (Hylander & Ehrlén 2013; Essl *et al.* 2015), the spatio-temporal path approach, as presented here, and its influences on the spatio-temporal legacy were, until now, not considered in landscape connectivity models. Studies that investigate the spatial-temporal legacy suggested that the relaxation time and its trajectory are affected by different resistance forces (Malanson 2002; James *et al.* 2007), and landscape connectivity is one of the most influential (Jackson & Sax 2009). We suggest that the spatio-temporal pathways, given its overarching positive influence in landscape connectivity, could significantly help to prevent species extinctions, especially in highly dynamic landscapes, such as most of the tropical ones. This could happen as highly dynamic landscapes also result in more spatio-temporal connected landscapes, which could facilitate rescue effect events (Brown & Kodric-Brown 1977), or remediate local losses with recolonizations (Kuussaari *et al.* 2009). Therefore, it also might have a strong influence on the duration, as well as in the trajectory of the relaxation time, and can partially be responsible for the overestimations of species extinctions due to habitat loss, usually attributed to time-lagged effects (Tilman *et al.* 1994). In summary, the increment of connectivity given the spatial dynamics could influence extinctions and recolonizations, which therefore could vary as a function of the amount of habitat that is available across a given period of time, and not only in a given snapshot time (Hanski 1999a). Such findings are contrary to what was previously suggested based on metapopulation studies, in which dynamic landscapes may experience more rapid declines in patch occupancy associated with habitat reductions, such that extinctions occur at higher levels of habitat (Wimberly 2006). Nevertheless, our study involves real landscape dynamics of tropical forests that could depart from simulated ones, particularly in terms of the spatial arrangement of stable and dynamic habitats (Matlack & Monde 2004), which could generate these differences.

We observed a positive curvilinear effect of the amount of habitat on spatio-temporal connectivity, with a peak in connectivity at around 30% of habitat (Fig. 4). For low amounts

of habitat, landscape connectivity plays a minor role, as habitat patches are usually so far apart that individuals rarely cross these large gaps; therefore, community composition and species abundance are more related to patch size than to connectivity (Martensen *et al.* 2012). In landscapes with reduced habitat coverage and connectivity, the spatial dynamics could be detrimental, as it might reduce overall habitat quality (younger habitat), while not being able to enhance connectivity (Wimberly 2006). At intermediate habitat amounts, the spatial dynamics could enhance landscape connectivity between more stable or to newly created patches, therefore increasing metapopulation survival probabilities (Matlack & Monde 2004; Wimberly 2006), as seen by the larger relevance of the PCstepst fraction in our case. In contrast, for larger amounts of habitat, where purely spatial connectivity is already high, and therefore habitats are already well connected, habitat dynamics could again reduce overall habitat quality, while not significantly increasing an already high landscape connectivity (Fig. 4).

The positive effect of spatio-temporal connectivity varies as a function of the percentage of habitat change, at least between 30% of habitat loss and 5% of habitat gain (Fig. 3a). With additional habitat gain, purely spatial connectivity surpasses the influence of spatio-temporal connectivity, and temporal aspects end up having no relevant influence. With net habitat loss, there is an increase in the importance of spatio-temporal connectivity, at least until 30% of habitat loss, which is the investigated range. Even in landscapes with a stable net amount of habitat, spatio-temporal connectivity has a positive influence on purely spatial connectivity, since the patchwork of losses and gains promotes an increase in effective connectivity of around 10%. However, this relationship might not be linear, and additional studies should investigate this further.

In our case study, we did not consider differences in habitat quality. Dynamic landscapes are known to drive forest habitats to early successional stages, since new habitats are constantly created, and more mature ones are lost (Teixeira *et al.* 2009). In dynamic landscapes, local extinction could

happen due to habitat destruction and overall reduction in habitat quality, whereas connectivity can provide access to newly created patches, partially compensating for these extinctions (Matlack & Monde 2004). Agricultural intensification is expanding over tropical regions, which has promoted large-scale spatial homogenization and reductions in landscape dynamics (Fahrig *et al.* 2011), which in turn can reduce spatio-temporal connectivity, while generating conditions for habitats to age. Habitat regeneration speed, species habitat requirements, and species life span all play important roles in these dynamics. We believe that our spatio-temporal model and corresponding metrics presented here could be extremely helpful in the understanding of this balance, and future efforts in this direction should incorporate information about habitat quality into node attributes.

Additionally, we observed that species dispersal capacity is directly related to how species are affected by the spatio-temporal dynamics, as larger dispersal capacities reduce the dependence on landscape connectivity to sustain populations in fragmented landscapes (Hanski 1999b). Nevertheless, we show that for species that could disperse up to 1000 m between habitats, which is greater than the dispersal capability of most tropical forest birds and small mammals species (Moore *et al.* 2008), the spatio-temporal dynamics of common tropical landscapes could significantly enhance landscape connectivity beyond what is predicted by purely spatial models. Therefore, we expect that for a large portion of tropical forest species, accounting for spatio-temporal effects is key for the understanding of their dynamics in fragmented landscapes, and the methods presented here could help in this endeavour. Moreover, in fast changing landscapes, as in most of the developing countries, and/or under climate change scenarios, species distribution modeling (SDM) could be largely tuned by incorporating fine scale spatio-temporal connectivity information in combination with broader scale dispersal patterns (Bled, Nichols & Altwegg 2013).

Lastly, we showed that most of the spatio-temporal connectivity happens through habitats that are lost or gained between time steps, which are used as stepping-stones (PCstepst) to move between stable or to newly created patches (Matlack & Monde 2004; Wimberly 2006). These dynamics are fundamental for linking habitat in a spatio-temporal context, by including connectivity that does not exist in a purely spatial perspective. This generates temporal directional connections, i.e. situations where patch A is connected to patch C, but C is not connected to A (Fig. 1c), differing from bidirectional spatial connections. This combination of unidirectional and bidirectional connections serves to mix populations and gene pools in a highly heterogeneous manner.

The study of landscape dynamics is particularly pressing in the current changing world (Auffret, Plue & Cousins 2015). Climate change is altering the speed of habitat regeneration in some regions (Whitmore 1998) and increasing disturbance (Dale *et al.* 2001). Increases in agricultural intensification are expected to reduce spatial and temporal heterogeneity, and large-scale spatio-temporal homogenization is already

happening in many regions (Fahrig *et al.* 2011). In summary, the type, rate and intensity of disturbances are changing, and therefore landscape dynamics are also changing (Turner 2010). To understand the effects of spatial dynamics and of these changes in dynamics is vital for fine-tuning the understanding of ecological processes and guiding landscape management. Changes in these dynamics could shorten relaxation time periods, or accelerate extinction debt effects. We believe that these are pressing questions, and that the model and metrics presented here are an important contribution for future applications and developments both in scientific and in management applications.

Authors' contributions

A.C.M. developed the conceptual model. S.S. designed the network model, adapted the connectivity metrics for the spatio-temporal case and developed the model scripts. A.C.M. applied the model and metrics in the study landscapes, analysed and summarized the results and developed the figures. A.C.M., S.S. and M.-J.F. conceived the ideas, wrote the paper and gave final approval for publication.

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Data accessibility

The original maps are available through the Dryad Digital Repository <https://doi.org/10.5061/dryad.p5t21> (Ribeiro *et al.* 2012).

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Supporting Information

Details of electronic Supporting Information are provided below.

Data S1. Martensen_et_al_sup_material.docx presents additional information about the maps and sampled landscapes, as well as additional figures of the results.

Data S2. Working_example.zip presents a complete working example of our model and scripts.