

Static Vs Dynamic Connectivity: How Landscape Changes Affect Connectivity Predictions in the Iberian Peninsula

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Research Article

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Abstract

Context Climate and land-use changes affect species ranges and movements. However, these changes are normally overlooked in connectivity studies, and this could have adverse consequences in the definition of effective management measures.

Objectives We evaluated two ways to incorporate this dynamism: (i) by acknowledging that connectivity is a fluctuating phenomenon (i.e., time-varying connectivity) and therefore, procuring long-term conservation measures; and (ii) by enhancing species movements to their future ranges (i.e., spatio-temporal connectivity). We further compared these dynamic approaches with traditional static connectivity methods.

Methods We compared the overall connectivity values and the prioritization of critical habitat patches according to the dynamic and static approaches. This comparison research was conducted for species associated with broadleaf forests of the different ecoregions of the Iberian Peninsula. We considered species habitat preferences for moving and a wide range of dispersal abilities to assess functional connectivity without focusing on a single species.

Results Static approaches generated varying overall connectivity values and priority patches depending on the time snapshot considered and different from those generated by dynamic approaches. The two dynamic connectivity approaches resulted in very similar priority conservation patches, indicating their potential to guide enduring conservation measures that enhance connectivity between contemporaneous habitat patches at multiple time snapshots but also species range shifts in time.

Conclusions Connectivity is affected by landscape changes, and only dynamic approaches can overcome the issues associated with these changes and provide valuable information to guide improved and enduring measures in changing landscapes.

1. Introduction

Landscapes change due to climate (Mora et al. 2013), and land-use variations (Song et al. 2018), and the natural dynamism of habitats. These changes may affect vegetation distribution and structure (Root et al. 2003; Beltrán et al. 2014), water availability (Taylor et al. 2013; Bishop-Taylor et al. 2018a), and other factors affecting species habitats. Changes in habitat distribution, amount, and quality may result in species' ranges shifts (among other responses such as phenological, behavioral, or genetic adaptation) to ensure species perdurance (Parmesan and Yohe 2003; Chen et al. 2011; Davidson et al. 2020; Román-Palacios and Wiens 2020). However, habitat fragmentation could complicate and even jeopardize species colonization of new areas with suitable habitat (Collinge 1996; Honnay et al. 2002). The enhancement of habitat connectivity is considered a key strategy to mitigate the detrimental effects of habitat fragmentation, as it eases the flow of resources, species, genes, and ecological processes through the landscape (Correa Ayram et al. 2015; Keeley et al. 2018a).

Changes in the spatial configuration, amount, and quality of species habitats, as well as the matrix in-between habitat patches, may alter the flow of species and ecological processes, involving changes in connectivity over time. Therefore, connectivity is increasingly recognized as a time-varying phenomenon (Keeley et al. 2018b; Zeller et al. 2020). Nevertheless, connectivity has traditionally been studied through a static and immutable approach, which identifies landscape areas that promote the exchange of individuals and processes between contemporaneous habitat patches (Nuñez et al. 2013; Albert et al. 2017; Costanza et al. 2020). Connectivity changes over time have been only recently incorporated into connectivity studies by analyzing landscapes at a unique future snapshot or multiple time snapshots (Saura et al. 2011; Beltrán et al. 2014; Bishop-Taylor et al. 2018b; Jennings et al. 2020). These studies have corroborated that connectivity is a dynamic phenomenon and does not remain constant over time. They usually identify stable areas (i.e., habitat patches or corridors) that persist with suitable conditions for the focal species over time as targets for conservation measures (the so-called climate refugia in the case of climate change). Considering connectivity as a time-varying phenomenon is important to adequately guide long-term management measures that enhance functional connectivity over a broad period of time.

So far, dynamic connectivity studies only considered changes in connectivity over time (i.e., time-varying connectivity) but rarely considered whether landscape features would allow the shift of species or processes at a specific snapshot to their future suitable ranges (Littlefield et al. 2017; Martensen et al. 2017; Carroll et al. 2018; Gray et al. 2020; Huang et al. 2020; Zhao et al. 2021). However, the distribution of species habitat and the surrounding landscape change, and the pattern of these changes may become a key factor to enable organisms to reach their future potential distribution areas. Thus, considering the connectivity between the different snapshots (i.e., spatio-temporal connectivity) might provide a step forward to allow more realistic, robust, and ecologically meaningful connectivity assessments. The scarce work reported on this topic was also greatly simplified as most studies did not account for particularities of the dynamism, the focal species, and/or the landscape. For instance, most of them did not consider network directionality (Acevedo et al. 2015), i.e., flow can only occur from a past to a future snapshot, and not in the opposite direction. Another usual simplification was connecting climate refugia. This implied considering climate as the only important factor in species habitat selection, although other variables as anthropic pressure or land cover are known to be of most importance in habitat selection (Mateo Sánchez et al. 2014; Gastón et al. 2019; Banfield et al. 2020). Other spatio-temporal connectivity assessments studied the connections between static protected areas; however, these areas might change (Elsen et al. 2020) and stop being suitable for species in the future. Furthermore, very few functional connectivity studies have accounted for the dynamism of landscapes and, at the same time, for species dispersal abilities and habitat preferences for movement (Keeley et al. 2018b; Zeller et al. 2020). In fact, most dynamic studies have disregarded the state and changes in the landscape matrix and how it impacts species movements, that is, the landscape resistance (Spear et al. 2010; Zeller et al. 2012; Mateo-Sánchez et al. 2015; Keeley et al. 2016). Integrating all these particularities would lead to an improved evaluation of spatio-temporal connectivity to comprehensively guide sound and feasible decisions for landscape management.

Importantly, and due to the limited resources allocated to conservation actions, it is essential to identify and focus efforts and means on the most critical landscape areas. A few time-varying and spatio-temporal connectivity studies prioritized conservation areas (Albert et al. 2017; Bishop-Taylor et al. 2018b; Jennings et al. 2020; Conlisk et al. 2021; Zhao et al. 2021). These studies mainly accounted for the perdurance in time of quality areas or their spatial probability of connection (i.e., effective distance). However, apart from these characteristics, it is important to regard the irreplaceability of the areas. In other words, consider whether alternative landscape elements could, at least partially, supplant the contribution to the overall connectivity of the considered area in case it gets lost or degraded. Some graph-based (Urban et al. 2009) habitat availability metrics have been proposed to include irreplaceability in connectivity prioritization: the Probability of Connectivity (PC) (Saura and Pascual-Hortal 2007; Saura and Rubio 2010), and the Equivalent Connected Area (ECA) (Saura et al. 2011; Santini et al. 2016), which have been proven to be good indicators to monitor landscape changes (Bishop-Taylor et al. 2018a; Poli et al. 2019; Keeley et al. 2021). Martensen et al. 2017 adapted these metrics to be applied in spatio-temporal connectivity studies. These newly customized metrics can be used to calculate the reachable habitat through spatial and temporal connections. Yet, these metrics have only been applied to calculate overall dynamic connectivity levels (Huang et al. 2020) and patches Betweenness Centrality (Zhao et al. 2021). These studies do not calculate the individual irreplaceability of landscape elements to identify key areas that promote species movements under changing conditions.

Our goal here was to gain insights about how to incorporate the dynamism in connectivity studies to (a) calculate overall connectivity and (b) prioritize individual habitat patches by their contribution to overall connectivity. For that purpose, we performed a quantitative and qualitative comparative study on the implications of three connectivity approaches: (i) static, (ii) time-varying, and (iii) spatio-temporal. Specifically, we compared the overall connectivity, and priority patches obtained from these three approaches in the time period from 1990 (initial snapshot, t1) to 2018 (final snapshot, t2). To do so, we focused on broadleaf forests along the different ecoregions of the Iberian Peninsula. We followed a functional approach (i.e., a resistance-based approach that accounts for species habitat selection) (Tischendorf and Fahrig 2000) in a multispecies framework (i.e., we considered a wide range of dispersal distances to capture the variable dispersal abilities of the species associated with the focal habitat). Therefore, this study also evaluated the change in connectivity for (a) species with different vagility (Costanza et al. 2020) and (b) among ecoregions with different ecological and climatic characteristics and trends (Olson et al. 2001). As far as we are aware, this study is the first analysis of time-varying and spatio-temporal connectivity that includes the mentioned particularities of the dynamism, the focal species, and the landscape matrix and prioritizes habitat patches by their contribution (or importance) and irreplaceability. Moreover, this work contributes to a more comprehensive understanding of the implications of incorporating dynamism in connectivity studies to guide more efficient and informed conservation planning.

2. Materials And Methods

2.1. STUDY AREA, ECOREGIONS, AND SPECIES

This study was carried out on the Iberian Peninsula (Fig. 1), South-Western Europe, an area especially affected by landscape changes (Loarie et al. 2009; Song et al. 2018). It has an extension of 581,000 km² and comprises two countries, Spain and Portugal. It is a heterogeneous area that encompasses very different ecological characteristics. Therefore, we divided the study area into biogeographic units or ecoregions with similar species, dynamics, and environmental conditions (Fig. 1, Table 1). This division was given by the terrestrial ecoregions of the world delineated by Olson et al. 2001. We hypothesized that species would only roam between habitat patches with similar ecological conditions. Therefore, we only considered the connections among habitat patches (i.e., broadleaf forests) belonging to the same ecoregion.

Table 1
Ecoregions of the Iberian Peninsula

ID	Ecoregion name	Area (km ²)
6	Cantabrian mixed forests	76366.89
8	Iberian conifer forests	34439.47
9	Iberian sclerophyllous and semi-deciduous forests	297966.58
15	Northeastern Spain and Southern France Mediterranean forests	27915.62
16	Northwest Iberian montane forests	57449.96
33	Pyrenees conifer and mixed forests	13419.41
19	Southeastern Iberian shrubs and woodlands	2710.95
21	Southwest Iberian Mediterranean sclerophyllous and mixed forests	70568.26

The diversity of focal species (i.e., broadleaf forest specialists) was represented by a wide range of median dispersal distances: 1 km, 2 km, 5 km, 10 km, 30 km, and 50 km. These distances condition species arrival to destination habitat patches and capture most dispersal abilities of terrestrial animals (Sutherland et al. 2000; Saura et al. 2011, 2017; Santini et al. 2013).

2.2. METHODS

We compared three different approaches to study connectivity: (i) static; (ii) time-varying; and (iii) spatio-temporal. The static approach (i.e., considering connections between contemporaneous habitat patches at a single time snapshot) was followed twice independently, one at an initial time snapshot t1 (1990) and another one at a final snapshot t2 (2018). These two static runs were denoted by s1 and s2 respectively. The time-varying approach (denoted by tv) considered together both time snapshots (t1 and

t2) just by comparing or adding the results of s1 and s2. This approach informed about how connectivity changed over time. Lastly, the spatio-temporal approach (denoted by st) studied the connection of habitat patches at t1 with those at t2. All analyses were developed separately for each ecoregion and dispersal distance.

The methods of this article are structured as follows (Fig. 2): Firstly, we defined the study scenarios (i.e., the combination of network and matrix characteristics) in section 2.3. To do so, we (a) identified the habitat patches (section 2.3.1), (b) calculated the resistance surface (section 2.3.2), (c) determined the connections between patches and its spatial probability of connection (section 2.3.3), and (d) calculated the temporal probability of the connections in the spatio-temporal scenario (section 2.3.4). Secondly, we carried out the connectivity analyses (section 2.4) to measure (a) the overall connectivity (section 2.4.1) and (b) the individual node importance to ultimately identify priority conservation patches (section 2.4.2). Lastly, we compared the connectivity results of each approach (static, time-varying, or a spatio-temporal), ecoregion, and dispersal distance.

2.3. SCENARIO DEFINITION: NETWORK AND MATRIX CHARACTERISTICS

We established three different scenarios (two static and one spatio-temporal) to represent the landscape (i.e., the combination of habitat network and matrix characteristics) for the different connectivity approaches. These scenarios encompassed: (a) the number, distribution, and area of focal habitat patches; (b) the characteristics of the surrounding matrix; (c) the spatial probability of connectivity between patches; and (d) the temporal probability of connectivity between spatio-temporal patches. These characteristics varied from t1 to t2, and therefore each run of the static approach (s1 and s2), as well as the spatio-temporal approach, had a different scenario associated. However, the time-varying approach did not require an additional scenario as it only considers together the two static approaches (i.e., scenarios).

2.3.1. Definition of habitat patches and nodes

Firstly, habitat cells were determined as the pixels covered by broadleaf forest at t1, t2, or both time snapshots according to CORINE land cover maps from 1990 and 2018. Subsequently, these habitat cells were classified as a) “stable” when identified as habitat at both time snapshots; b) “lost” if they were identified only at t1, and c) “gained” when identified only at t2. We then delineated habitat patches as contiguous habitat cells with the same temporal classification (stable, lost, or gained) with a surface over 50 ha. This big patch size threshold was set for two reasons: firstly, to ensure that patches can host individuals throughout their entire lifetime to overcome species connectivity over generations (Keeley et al. 2018) and secondly, for feasible computational processing. The resulting habitat patches defined the network nodes (Urban et al. 2009), which were qualified by their area (i.e., patch attribute). We used the whole set of nodes under the spatio-temporal scenario. However, we only used stable and lost nodes in the initial static scenario, while stable and gained nodes in the final static scenario (Fig. 3).

2.3.2. Landscape matrix characterization: Resistance surface

Next, the landscape matrix of each scenario was characterized through resistance surfaces (Tischendorf and Fahrig 2000; Spear et al. 2010; Zeller et al. 2012). These surfaces depicted how the landscape allowed or impeded species movement. To create them, we assigned different resistance values to each land cover class/use according to Table S1 (in the supplementary data) based on previous studies of forest species in Spain (Gurrutxaga et al. 2011; Ruiz-González et al. 2014; de la Fuente et al. 2018) and expert opinion. These resistance values ranged from 1 to 1000, with increasing values corresponding to classes that restrain forest species movement. Resistance surfaces for the initial and final static scenarios were created from CORINE land cover maps at t1 and t2 respectively combined with the distribution of roads from OpenStreetMap (www.openstreetmap.org) to include the influence of linear infrastructures in species movements (Banfield et al. 2020). On the other hand, the resistance surface of the spatio-temporal scenario was defined as the mean of the two static surfaces. All resistance surfaces were processed at a spatial resolution of 200 m.

2.3.3. Connections between nodes: spatial probability of dispersal

We applied least cost path modeling (Adriaensen et al. 2003) to determine the connections among nodes centroids with the R package gDistance. For each scenario, we connected each node with all the nodes of the same ecoregion. The effective distance of these connections (i.e., the accumulated resistance along the least cost path) depicted the difficulty of moving between each pair of nodes through the resistance surface. These effective distances were then converted into probabilities of direct spatial dispersal between each pair of nodes (Appendix S1). This conversion was calculated as the negative exponential function of the effective distance between patches (Saura and Pascual-Hortal 2007; Gurrutxaga et al. 2011; Saura et al. 2017, 2018). This function was adjusted to the dispersal abilities of the focal species by assigning a probability of 0.5 to the species median effective dispersal distance. To estimate the species median effective dispersal distance, we multiplied the previously defined lineal dispersal distances (i.e., 1, 2, 5, 10, 30, 50 km) by the median landscape resistance value (Gurrutxaga and Saura 2013) of the spatio-temporal scenario. Finally, we excluded the connections with a spatial probability of connectivity below 0.001 and obtained a set of viable connections between nodes with their spatial probability of connection for each scenario and dispersal distance. We used R software for the calculations.

2.3.4. Spatio-temporal adjustment of connections: temporal probability of dispersal

In the spatio-temporal scenario, aside from the spatial probability of dispersal, we incorporated a temporal component (i.e., the temporal probability of dispersal between nodes) (Martensen et al. 2017). On the one hand, this temporal component (Table 2 and Fig. 3) dealt with the directionality of the

network: successful direct spatio-temporal connectivity only occurred with the connection of patches active at an initial time t1 with patches active at a later final time t2. These links only existed in this forward direction, as it is impossible to move from future to past patches. Therefore, links that started at a gain node or ended at a loss node were associated with a null temporal probability of connectivity. On the other hand, the temporal component also depicted nodes coexistence: species could only move between contemporary patches that are active simultaneously at any intermediate time. In this respect, links starting and/or ending at stable nodes had an associated temporal probability of 1, as the starting and ending nodes were sure to coexist during a certain period of time. Finally, links starting at a loss node and finishing at a gain node had an associated temporal probability of 0.5, since their coexistence cannot be assured. However, we did not examine the length of the overlapping time period, which could modify this probability. To incorporate this temporal component in the spatio-temporal scenario we multiplied the spatial probability by the temporal probability of connectivity of each link. It resulted in the spatio-temporal probability that an individual moves from a given node at t1 to another node at t2.

Table 2
Temporal probability of connectivity from a source node at t1 (1990) to a destination node at t2 (2018).

		Destination node		
		Stable	Lost	Gained
Source node	Stable	1	0	1
	Lost	1	0	0.5
	Gained	0	0	0

2.4. CONNECTIVITY ANALYSES

We performed a comparative assessment of the analyzed approaches (static, time-varying, and spatio-temporal) and the different ecoregions and dispersal distances. To do so, we calculated and contrasted the following connectivity analyses: i) the overall connectivity of the network (section 2.4.1), and ii) prioritization of key habitat patches to maintain the connectivity (section 2.4.2). To analyze connectivity, we used graph-based habitat availability metrics (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010), which integrate intrapatch connectivity (habitat available within habitat patches) with interpatch connectivity (habitat reachable through connections between patches). All connectivity metrics were calculated with the command line Conefor software (Saura and Torné 2009, www.conefor.org). The spatio-temporal scenario required the version for directed networks.

2.4.1. Overall connectivity

We used the Equivalent Connected Area (ECA, Saura et al. 2011; Santini et al. 2016) to determine the overall level of connectivity of each ecoregion, scenario, and dispersal distance. ECA (Table 3) is defined as the area of a single habitat patch that would provide the same amount of connectivity (probability of connectivity or PC, Table 3) as the actual pattern of habitat patches in the whole landscape. We calculated the ECA for the two static scenarios (ECA_1 at t_1 and ECA_2 at t_2), while for the spatio-temporal one we used a dynamic adaptation of this metric (ECA_{st}) (Martensen et al. 2017), best suited for the particularities of this scenario. The ECA of the entire study area was calculated as the sum of the resulting ECA value of each ecoregion. Afterward, we calculated the connectivity change (dECA, Table 3): (a) from the initial to the final static scenario (dECAtv) to measure the changes in connectivity over time (time-varying connectivity); and (b) from the initial to the spatio-temporal scenario (dECAst) to measure the difference in connectivity between following a static and a spatio-temporal approach. ECA and dECA metrics have area units and thus can be easily interpreted and compared with the existing focal habitat area, and its variation dA (Table 3) (Saura et al. 2011).

Table 3

Metrics description. The metrics subindices represent the approach: 1 for the initial static approach in 1990; 2 for the final static approach in 2018; tv for the time-varying, and st for the spatio-temporal approach. For details on PC and ECA metrics see Saura 2007; Saura and Rubio 2010 and Martensen et al. 2017 for details on the spatio-temporal adaptation.

Metric (units)	Description
A (ha)	Focal habitat area. Calculated at t1 (A_1) and t2 (A_2)
$dA = \frac{A_2 - A_1}{A_1} \cdot 100$ (%)	Focal habitat area change: Percentage of increase/decrease in habitat area between t2 and t1
PC	Probability of Connectivity: Probability that two randomly selected points within the landscape fall into spatially connected habitat patches. Calculated at t1 (PC_1) and t2 (PC_2)
PC_{st}	Spatio-temporal Probability of connectivity: Probability that two randomly selected points within the landscape, one at t1 and the other one at t2, fall into spatially and temporally connected habitat patches.
dPC	Relative importance of each node to overall connectivity. Calculated for every approach: dPC_1 , dPC_2 , dPC_{tv} , and dPC_{st} .
ECA (ha)	Overall connectivity: Equivalent Connected area or area of a single habitat patch that would provide the same PC as the actual pattern of habitat patches in the whole landscape.
ECA_{st} (ha)	Spatio-temporal overall connectivity: the area of a single stable habitat patch that would provide the same PCst as the network composed of the set of lost, gained, and stable habitat nodes of the landscape
$dECA_{tv} = \frac{ECA_2 - ECA_1}{ECA_1} \cdot 100$ (%)	Connectivity change in the time-varying approach: Percentage of increase/decrease in the connected habitat area from t2 to t1
$dECA_{st} = \frac{ECA_{st} - ECA_1}{ECA_1} \cdot 100$ (%)	Connectivity change in the spatio-temporal approach: Percentage of increase/decrease in the connected habitat area from the spatio-temporal to the initial static scenario.

2.4.2. Identification of priority habitat patches

To characterize patches importance, we used the relative variation in the metric PC (dPC , Table 3) when systematically removing each habitat patch (Saura and Pascual-Hortal 2007). The patches with the highest dPC are the most important and irreplaceable to maintain the overall landscape connectivity, and therefore should be considered as critical and priority elements. To facilitate comparability between ecoregions and approaches, we integrated the patch importance of all dispersal distances considered (i.e., to account for the diversity of species associated with the focal habitat). For this purpose, we min-max normalized and summed the individual importance of all dispersal distances. We obtained a generalized relative importance for each patch and scenario (dPC_1 , dPC_2 , and dPC_{st} for the static at t1, static at t2, and spatio-temporal scenarios respectively). We used separately dPC_1 and dPC_2 to inform

about patches importance in the two static approaches, however, we summed these two metrics to measure the time-varying connectivity importance (dPC_{tv}).

Finally, to select the priority patches of each ecoregion and approach we identified the patches with the highest generalized relative importance whose area sum less than 10% of the total ecoregion area. To ensure comparability between the three connectivity approaches, we selected two sets of priority patches for each of the two dynamic approaches (time-varying and spatio-temporal), one including only patches active at t_1 , and another one with patches active at t_2 . In this way, six sets of priority patches were created ($Prior_1$, $Prior_2$, $Prior_{tv_1}$, $Prior_{tv_2}$, $Prior_{st_1}$, and $Prior_{st_2}$). To compare the prioritization through the different connectivity approaches, we calculated the percentage of priority area shared by the six sets of priority patches. These percentages of shared priority area were calculated for each ecoregion and for the whole study area by summing the priority areas of every ecoregion.

3. Results

3.1. Changes in the topology of the habitat network over time.

There was a general increase in broadleaf forest area (dA) in the Iberian Peninsula of 40.11% (Table S2, Fig. 4), covering 11 and 15% of the study area in 1990 and 2018 respectively. Most of the habitat was classified as gained (absent at t_1 and present at t_2), followed by stable and lost (Fig. 4). Most ecoregions experienced an increase in the total habitat area and the mean patch size (Table S2). Only ecoregion 21 (Southwest Iberian Mediterranean sclerophyllous and mixed forests) showed a decrease in its total habitat area and mean patch size. The ecoregion 19 (Southeastern Iberian shrubs and woodlands) did not have any habitat patch in 1990 and only a small patch in 2018, therefore we did not present the results of this ecoregion. Inland Iberian ecoregions (Iberian sclerophyllous and semi-deciduous forests, and Iberian conifer forests ecoregions, i.e., ecoregions 9 and 8) had the smallest relative habitat area (i.e., the proportion of area covered by habitat) and the smallest mean habitat patch size at both time snapshots. Despite the total increase in habitat, the results also showed that there was a degradation or loss of quality of the surrounding landscape matrix for the movement of focal species: the mean resistance of the study area increased from 72.32 to 81.28.

3.2. Static connectivity

As expected, the overall connectivity (ECA) increased with the dispersal abilities of the species (Fig. 5) at both s_1 and s_2 static scenarios. This growth in connectivity is more notable in low to medium dispersal distances (from 1 to 20km). Priority patches drastically differed between static scenarios (Table S3, Fig. s4). In fact, only 35.9% of the final priority patches (at t_2) of the entire study area were identified as a priority in the initial scenario (at t_1). This percentage of shared priority habitat area between the two static scenarios varied between ecoregions from 0 to 60.7% in Cantabrian mixed forests (ecoregion 6), and Southwest Iberian Mediterranean sclerophyllous and mixed forests (ecoregion 21) respectively.

3.3. Time-varying connectivity

The overall connectivity (ECA) showed a mean increase of 39.57% (standard deviation of 1.2) from 1990 to 2018 for all dispersal distances (Fig. 5). This connectivity change ($dECA_{tv}$) remained positive and stable across all dispersal distances, and with a very similar magnitude to the habitat area change (dA) when considering the whole study area (Fig. S1). However, most ecoregions showed a higher increase in overall connectivity for species with low dispersal capacity (Fig. S2), indicating that vagile species are less sensitive to changes in connectivity. In fact, in most ecoregions, this increase in overall connectivity was greater than the increase in total habitat area for short dispersal distances, while it was similar or smaller for large dispersal distances (Figure S3). On the contrary, ecoregions 6 (Cantabrian mixed forests), 8 (Iberian conifer forests), and 21 (Southwest Iberian Mediterranean sclerophyllous and mixed forests) showed a larger increase in habitat area than in overall connectivity. Particularly, this last ecoregion was the only region that experienced a decrease in habitat connectivity. The priority areas identified when following a time-varying approach covered a mean of 99.8 and 98.7% of the priority area from the initial and final static scenarios respectively (Table S3 and Fig. S4).

3.4. Spatio-temporal connectivity

The overall connectivity in the spatio-temporal scenario (ECA_{st}) was in an intermediate state between the two static scenarios for all dispersal distances (Fig. 5). As in the static scenarios, the spatio-temporal overall connectivity increased with the dispersal distance for species with limited dispersal capabilities and remained almost stable for medium and large dispersal distances. Generally, there was a positive connectivity change ($dECA_{st}$) (Fig. S1) which highlights the connectivity gain from t_1 to t_2 . Most ecoregions also followed this trend (Fig. S5), yet ecoregions 8, 16, and 21 (Iberian conifer forests, Northwest Iberian montane forests, and Southwest Iberian Mediterranean sclerophyllous and mixed forests) had less connectivity in the spatio-temporal scenario than the initial static scenario, as shown by the negative connectivity increase. This last ecoregion experienced a loss of both habitat and connectivity, and thus, this negative change in connectivity was expected. However, ecoregions 8 and 16 presented an increase in habitat and connectivity from 1990 to 2018 when not considering the spatio-temporal dynamism.

Priority nodes identified in the spatio-temporal scenario matched closely with those from the static scenarios (Table S3 and Fig. S4 in the supplementary data). A mean of 98.9 and 97.9 % of the priority patches in the initial and final static scenarios were also detected as priority areas in the spatio-temporal scenario. Therefore, the results of spatio-temporal connectivity identified priority conservation areas to ensure species range shifts, but also the maintenance of connectivity in specific snapshots in a varying landscape network. Additionally, 97% of the time-varying priority area was also identified as a priority when following the spatio-temporal approach. That is to say, the resulting key conservation areas were almost the same in the two approaches that account for the landscape dynamism.

4. Discussion

The abundant evidence of climate (Mora et al. 2013) and land-use changes (Song et al. 2018), and their influence on species distribution (Parmesan and Yohe 2003; Chen et al. 2011; Davidson et al. 2020) highlight the need to incorporate the landscape dynamism in conservation studies. Understanding how these landscape changes influence species connectivity is an important step forward in contemporary connectivity research and conservation planning. Habitat availability indices have been shown to be very useful for quantifying overall connectivity and identifying critical elements to maintain or enhance it. However, so far, they have been mainly used under a static approach (Dondina et al. 2017; de la Fuente et al. 2018; Cisneros-Araujo et al. 2021). Nevertheless, they have enormous potential to be adapted to different spatial and temporal probabilities of connectivity and deal with the directionality of the links. Therefore, they are a sound option to account for dynamism in connectivity analyses. This work aimed to gain insights into the use of these indices under two different dynamic approaches and to assess potential conceptual and practical differences among them and with traditional static approaches. Furthermore, the variety of considered ecoregions and species (i.e., dispersal abilities) allow a comprehensive interpretation of the results to advance in the incorporation of functional connectivity concerns for a wide array of species in changing landscapes. Therefore, this study may set a practical example to guide other analyses within a different management context (i.e., different study areas, focal species, landscape changes, and time snapshots). Particularly, the framework here exposed may be applied to future projections which would allow conservationists to anticipate future landscape changes and to implement improved measures with more functional and enduring conservation results.

4.1. Changes in the topology of the habitat network over time

We found a generalized increase in the broadleaf forest area in the Iberian Peninsula. This growth is consistent with other studies that found a net forest gain in the last years in Europe, and specifically in Spain and Portugal (FAO 2015), and all the biomes found in the Iberian Peninsula (Song et al. 2018), but especially in mountainous (ecoregions 33, 16, and 8) and temperate oceanic regions (ecoregion 6). However, this increase in forest area differs from other studies that found an overall forest loss in Spain and Portugal (Hansen et al. 2013). Nevertheless, all these previous studies examine general forest change rather than focusing only on broadleaf forests. Mixed or coniferous forest areas may have changed to broadleaf, appearing as habitat gain only in this study. Other possible causes of discrepancies might be the definition of forest area and the spatial and temporal resolution.

This broadleaf forest increase might be the result of recent agricultural land abandonment, afforestation activities, conservation policies, and the establishment of tree plantations. However, this net increase does not account for habitat quality. The gain of early successional or low heterogeneity forests may exceed the loss of mature and diverse forests, but not completely replace the ecosystem processes. In fact, many mature pure stands may be transformed into mono-species plantations (Teixido et al. 2010). These areas would be considered here as stable habitat patches besides the great loss of biodiversity and habitat quality.

4.2. Time-varying connectivity: Differences in connectivity between two snapshots

The results confirm that connectivity changes over time as given by the varying value of overall connectivity (Fig. 5) and the different priority habitat patches between the two snapshots (Table S3 in supplementary material). These changes should be accounted for when planning optimal conservation measures to lengthen the beneficial effects of the measures. In this study, landscape changes in habitat amount and distribution and in the surrounding matrix resulted in a large improvement in connectivity in the period analyzed from 1990 to 2018. There was a slightly larger increase in connectivity than in the total focal habitat area (Fig. S2). This might indicate that the habitat patches in 2018 were better connected because of the added habitat area per se (intrapatch connectivity) but also due to additional or improved connections between patches (interpatch connectivity). These improved connections might be the result of the gained habitat patches enhancing the connections with and between stable patches, or due to better characteristics of the intermediate matrix (even though there is an overall resistance increase, the matrix might have improved in-between the two connecting patches).

We found that landscape changes in most ecoregions had bigger impacts in connectivity for species with low dispersal distances (Fig. S2 in supplementary data): the gained or improved connections seem to be especially beneficial to short dispersers (Saura et al. 2011). Therefore, gained habitat patches may have been located close to the stable patches, acting as stepping stones and improving interpatch connectivity mostly for short dispersers. On the other hand, connectivity changes for vagile species were similar to the variation in habitat area. This might justify the focus of connectivity analyses in species with low dispersal abilities, which are more sensitive to landscape changes.

4.3. Spatio-temporal connectivity: connectivity between different time snapshots

Unlike static and time-varying approaches, spatio-temporal studies focus on connections between different snapshots. Following other approaches might lead to misjudging species connectivity to their future ranges in changing landscapes. The differing results obtained from static and spatio-temporal connectivity approaches suggest that static approaches fail to account for the connectivity between snapshots. The overall connectivity according to the spatio-temporal approach was in between that of the two static approaches, being in this case study generally smaller in 1990 and larger in 2018. Thus, the landscape changes (in the habitat patches distribution and area and the surrounding matrix) led to a large final static connectivity that did not especially favor the spatio-temporal connectivity between the two time snapshots (Fig. 2). The resulting final static overall connectivity tended therefore to overestimate spatio-temporal connectivity. However, when there was habitat loss (ecoregion 21, Southwest Iberian Mediterranean sclerophyllous and mixed forests) the use of static approaches underestimated the connectivity between snapshots. The same pattern of over and underestimation with net habitat gain and loss was found in other studies (Martensen et al. 2017; Huang et al. 2020).

The connectivity difference between the initial static and the spatio-temporal approaches decreased with the species dispersal distance (Figs. S1 and S5): species with low dispersal distances were more benefited from the spatio-temporal perspective than vagile species. This pattern was also found in other spatio-temporal connectivity studies (Martensen et al. 2017) and when comparing time-varying and static approaches (Fig. S2). This trend was particularly noticeable in Northwest Iberian montane forests (ecoregion 16), which even presented a loss in spatio-temporal connectivity for large dispersal distances (Fig. S5) despite the increase in habitat area (Table S2). This may be caused by the loss of links or stepping stones that connected distant nodes, which hindered the movement of long-distance dispersers. At the same time, the new habitat might have appeared close to other habitat patches already reachable for good dispersers and only enhancing the movement of species with low dispersal capacities.

When incorporating the temporal component to the probability of dispersal between patches Martensen et al. 2017 considered the auxiliary links aside from the direct links here accounted. These auxiliary links do not provide spatio-temporal connectivity by themselves as they do not connect nodes active at t_1 with nodes active at t_2 (i.e., auxiliary links start at a gained node or finish at a lost node). However, they connect nodes that could coexist in time. The connection of these auxiliary links with other links could result in actual spatio-temporal connectivity. We did not consider this kind of link in our study, as their inclusion did not change the results and highly increased computing times.

4.4. Patch prioritization

The results show substantial differences in habitat prioritization between the two static approaches (Table S3 and Fig. S4). The key areas that maintain connectivity among contemporary patches largely varied from the initial to the final snapshots. Therefore, relying on traditional static connectivity models may lead to the prioritization of temporal suitable areas that would not persist under this condition for a long period. This finding further strengthens the idea of connectivity as a time-varying phenomenon (Saura et al. 2011; Beltrán et al. 2014; Bishop-Taylor et al. 2018b; Jennings et al. 2020).

The two dynamic approaches adopted here (i.e., time-varying and spatio-temporal) promote connectivity between coexisting patches at several snapshots and from past to future patches. Even though the two approaches accounted for landscape dynamism differently, they identified almost the same priority patches (Table S3, Fig. S4). That is to say, the patches with the highest long-term importance also contributed to a larger extent to species movements to their future ranges. The two dynamic approaches also captured neatly the priority areas from static scenarios at the two snapshots. Dynamic prioritization approaches are therefore useful to identify the key patches to promote connectivity at specific time snapshots, but they give extra consideration to patches critical at other time snapshots or with important spatio-temporal connections. However, only the spatio-temporal connectivity approach addresses all these issues running a unique model that remains useful despite changes in the landscape, while the time-varying prioritization approach requires running one model per time snapshot considered.

5. Conclusions

This study emphasizes the importance of considering the dynamism of changing landscapes in connectivity studies. Traditional static approaches did not accurately assess the impacts of these changes. We have seen two different ways to incorporate the dynamism in connectivity studies: a) by acknowledging that connectivity is a time-varying phenomenon and therefore, procuring long-term conservation measures; and b) by enhancing species movements from their past to future ranges. We have shown that following different connectivity approaches resulted in very different overall connectivity values. Therefore, it is important to select the appropriate approach depending on the study objectives and the dynamic perspective considered. Otherwise, we might over or underestimate the connectivity levels in and between different time snapshots. On the other hand, habitat patches prioritization by means of the two dynamic perspectives showed very similar results. Both of them also identified most of the priority areas from static approaches at the two snapshots considered. Therefore, conservation strategies based on the two dynamic prioritization approaches may equally deal with the dynamism of landscapes and still enhance traditional static connectivity. That is to say, following either approach to incorporate the dynamism would foster enduring conservation measures that enhance connectivity between contemporaneous habitat patches, but also species range shifts in time. However, further research in this direction is needed to draw conclusions in other study areas, landscape changes, and time windows.

Declarations

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Competing interests

The authors declare that they have no competing interests

Ethics approval and consent to participate

Not applicable. However, authors comply with the IUCN Policy Statement on Research Involving Species at Risk of Extinction.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The data that support the findings of this study are openly available at <https://land.copernicus.eu/pan-european/corine-land-cover>.

Code availability

The scripts used to generate the analyses presented are available in “figshare” at <https://figshare.com/s/b9411312d964895deac3>, DOI 10.6084/m9.figshare.16799503 .

Authors contribution

All authors conceived the ideas and designed the methodology; TG analyzed the data and ran the connectivity models with help from MCM. TG led the writing of the manuscript and MCM reviewed it thoroughly. Both authors contributed critically to the drafts and gave final approval for publication.

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Figures

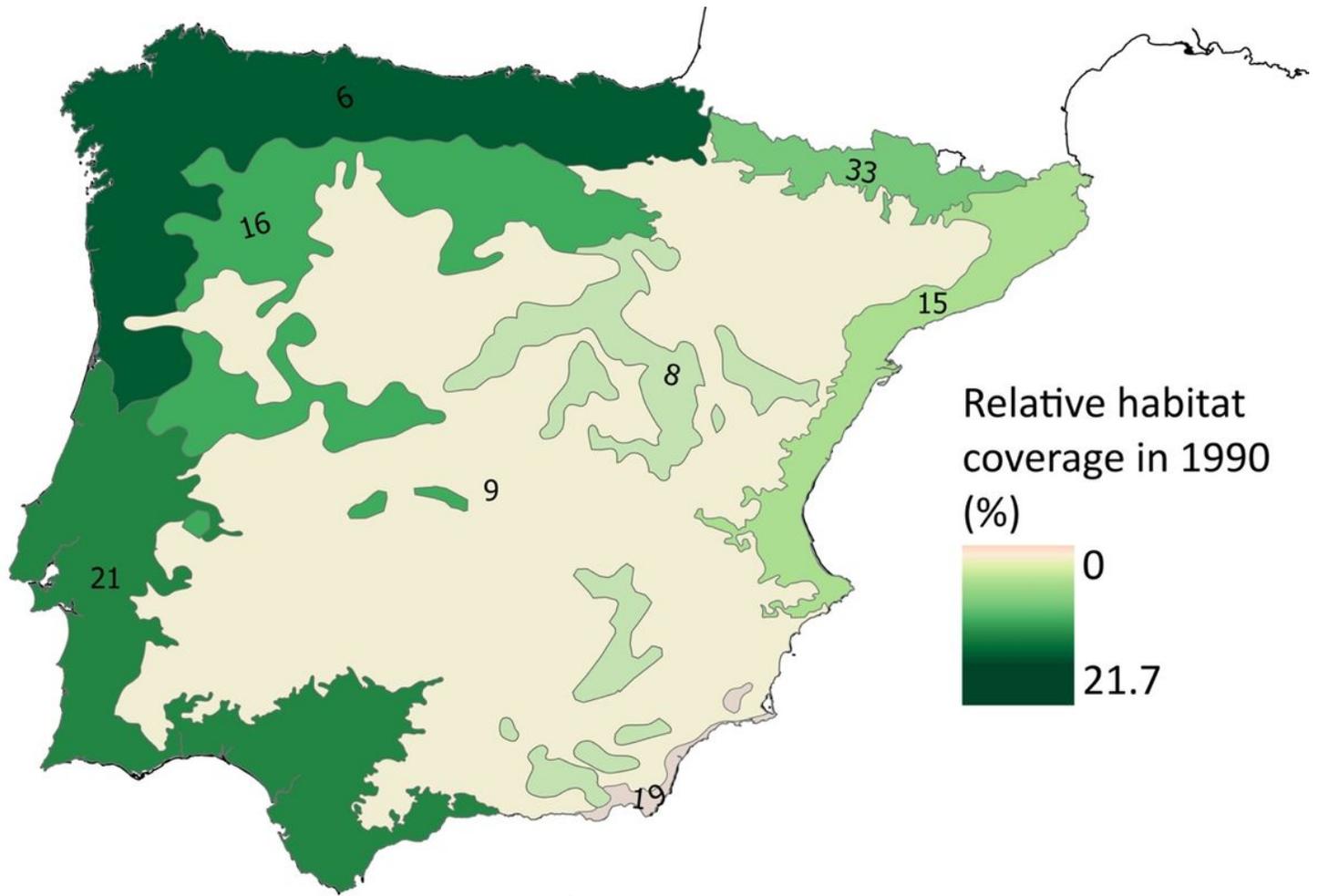


Figure 1

Ecoregions of the Iberian Peninsula and their relative habitat coverage (i.e., percentage of ecoregion area covered by broadleaf forest) in 1990. Ecoregions names can be found in Table 1.

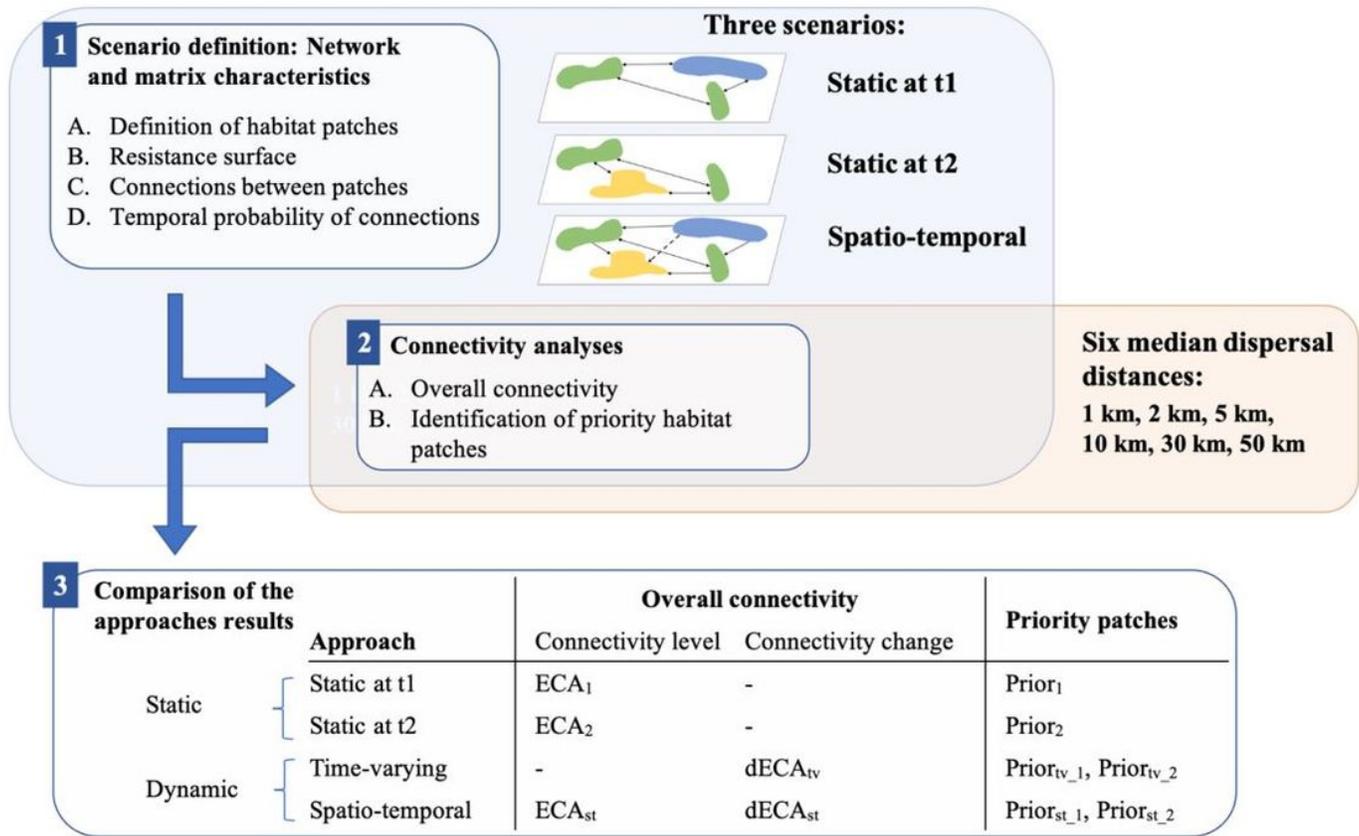


Figure 2

Methodological workflow scheme. 1. Scenario definition (section 2.3): We developed three scenarios, i.e., the combination of network and matrix characteristics: static at t1 (1990), static at t2 (2018), and spatio-temporal from t1 to t2. To do so, we (a) identified the habitat patches, (b) calculated the resistance surface, (c) determined the connections between patches with least cost path modeling and the spatial probability of connection, and (d) calculated the temporal probability of the connections. This was done separately for the three scenarios. 2. Connectivity analyses (section 2.4): we calculated different connectivity metrics (Table 3) to measure: (a) the overall connectivity and (b) the individual patch importance to ultimately identify priority conservation patches. This second stage was conducted for the three scenarios and six dispersal distances. 3. Comparison of connectivity approaches: We compared the connectivity results when following a static, time-varying, or spatio-temporal approach.

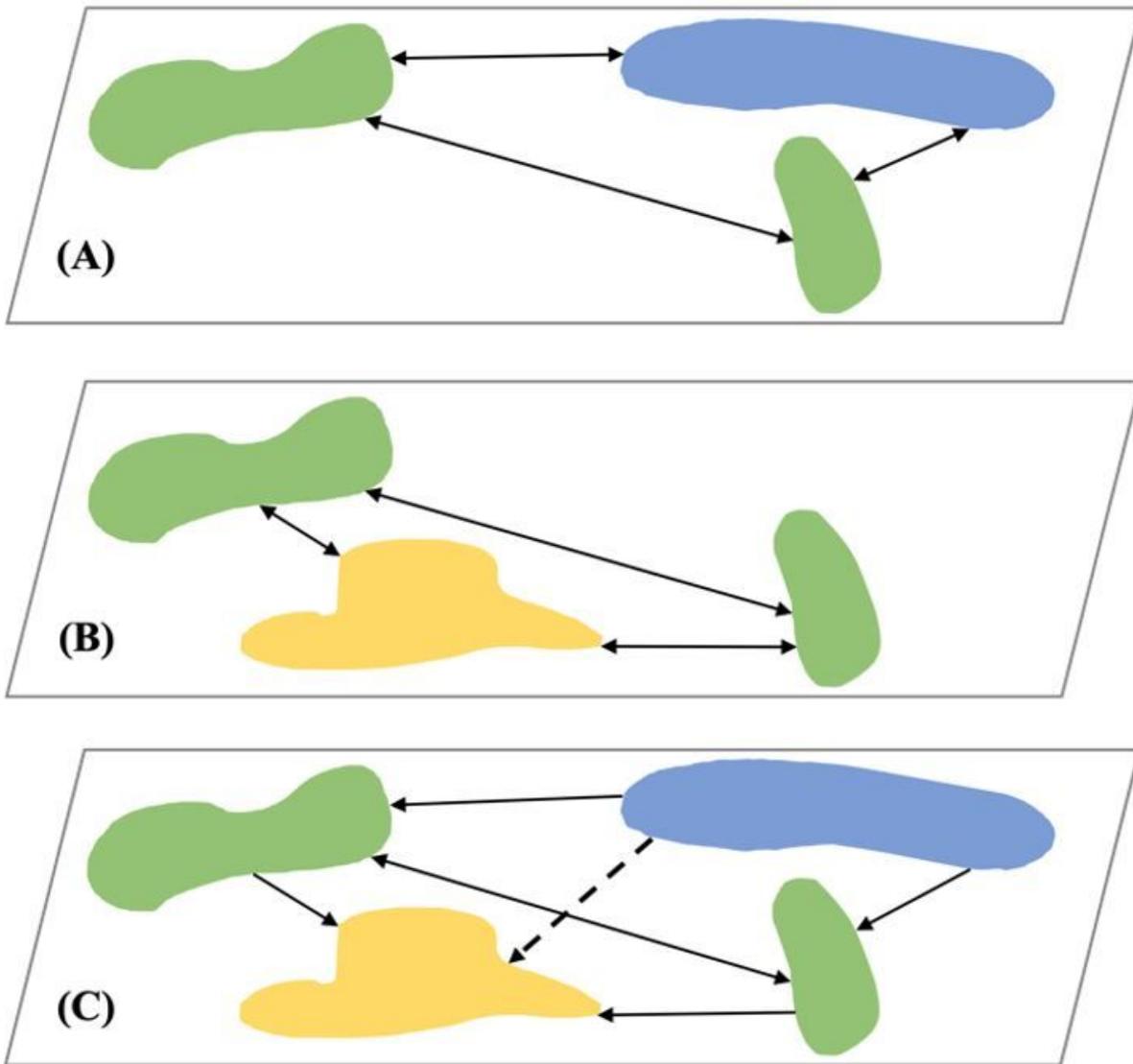


Figure 3

Representation of the habitat patches and connections between them for the three scenarios: (A) static at t1 (1990); (B) static at t2 (2018); and (C) spatio-temporal from t1 to t2. Stable (active at t1 and t2), lost (active at t1), and gained (active at t2) patches are represented as green, blue, and yellow shapes respectively. One and two-way arrows represent the possible links and the direction of the connection between nodes. All the connections in the static scenarios (A and B) are bidirectional, while they are directed in the spatio-temporal scenario (C), only connecting nodes active at t1 (stable and lost) with nodes active at t2 (stable and gained). Solid and dashed arrows in the spatio-temporal scenario denote the temporal probability nodes coexistence of 1 and 0.5 respectively.

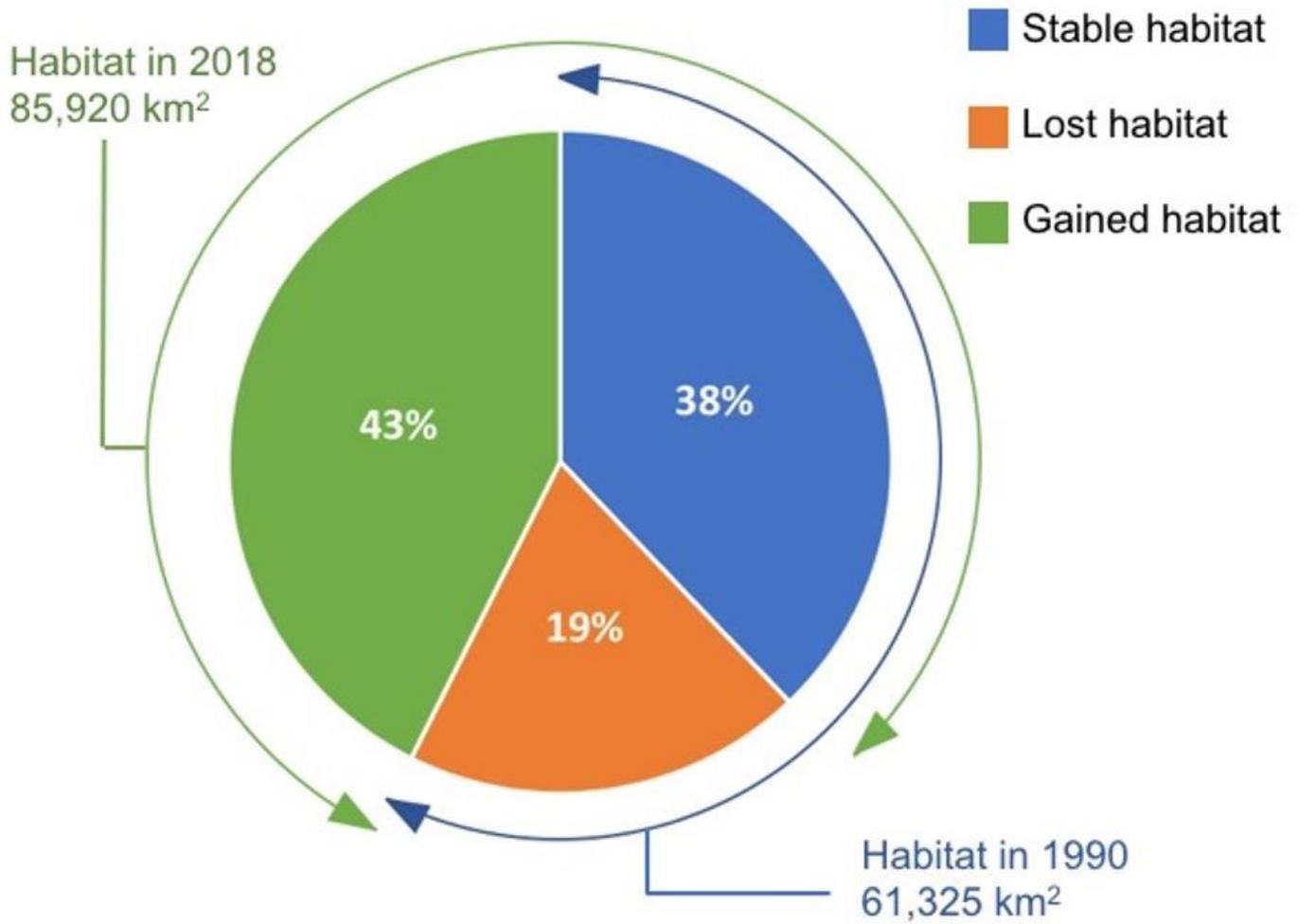


Figure 4

Proportion of each habitat class (stable, lost, and gained) in the Iberian Peninsula, and total habitat (deciduous forest) area in 1990 and 2018.

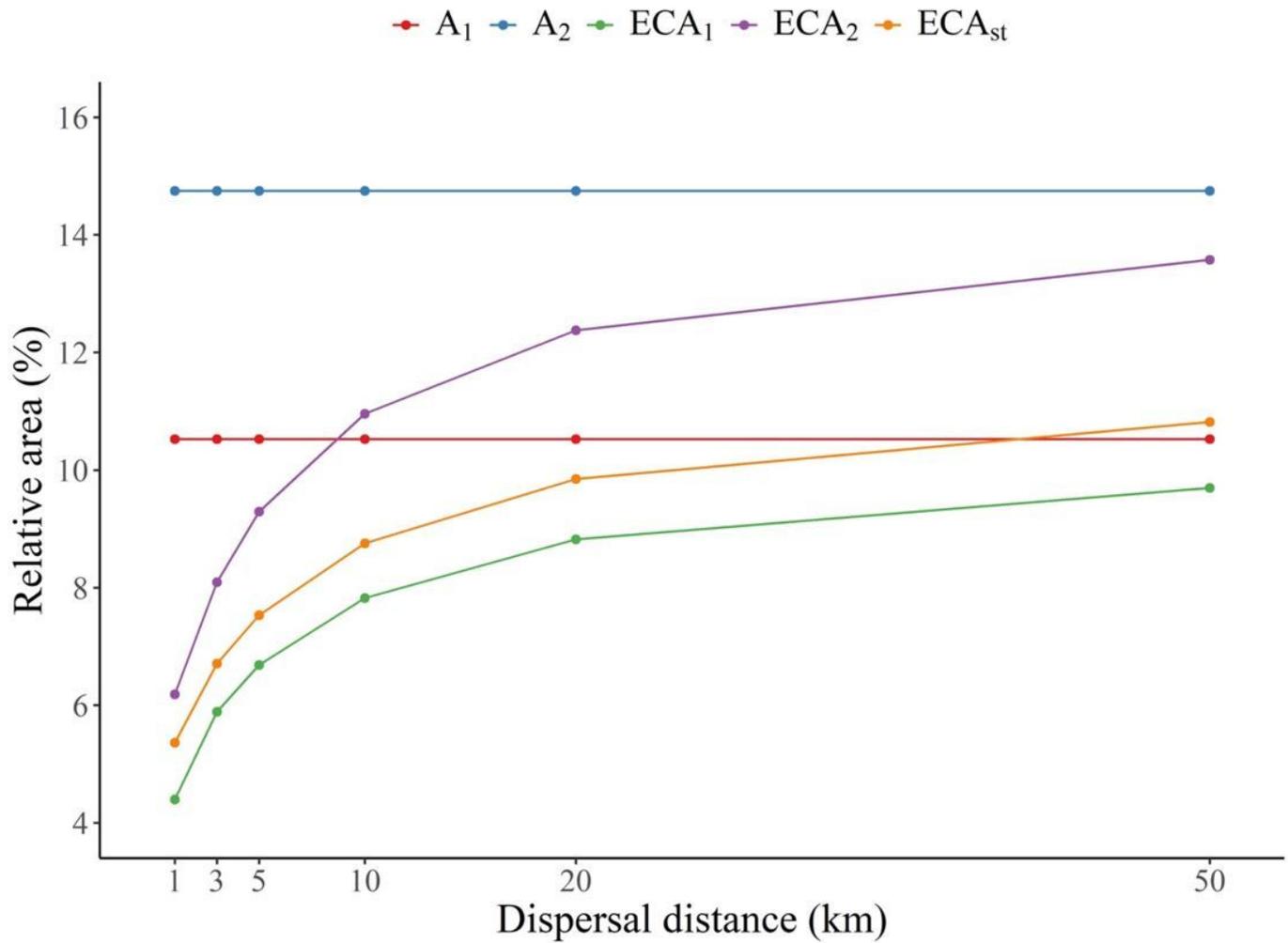


Figure 5

Relative habitat area and overall connectivity: Percentage of study area covered by focal habitat (A) and by connected habitat (ECA) in the initial static (in 1990, subscript 1), final static (in 2018, subscript 2), and spatio-temporal (subscript st) scenarios.

Supplementary Files

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