RESEARCH ARTICLE

Assessment of habitat connectivity in a highly fragmented ecosystem: The seasonal tropical dry forest in Ecuador

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Abstract

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Context: Connectivity is a parameter that plays a fundamental role in highly fragmented ecosystems, such as the seasonal tropical dry forest.

Objectives: The objective of this research is to calculate the evolution of fragmentation and the functional connectivity of the Ecuadorian seasonal dry forest from 1990 to 2018, and to compare the Ecuadorian state's reforestation plan with our reforestation plan, which is based on maximising connectivity with the smallest possible reforested area.

Methods: The land cover changes, fragmentation and functional connectivity, measured by employing cumulative cost analyses at three different distances (0.5, 5 and 10 km), that occurred in Ecuadorian seasonal dry forests between 1990 and 2018 were verified using GIS environments, vector layers and Graphab software. A reforestation plan was also developed using various connectivity metrics and was then compared with that proposed by the Ecuadorian Ministry of the Environment.

Results: Between 1990 and 2018, 2647 km² of dry forest was lost in the study area. Former forest areas were put mainly to agricultural uses, which increased by 12.96%. The total number of patches decreased from 6908 to 5357, signifying a loss of 30% of the forest area and leading to losses of up to 75% of connectivity. Areas with low connectivity and a risk of disappearance were identified, and a new reforestation plan was proposed, which was based on maximising connectivity with small patches.

Conclusions: Because of the fragmentation, the connectivity of the seasonal dry forest in Ecuador is dramatically decreasing in the last decades. Therefore, the reforestation plans should prioritise areas whose reforestation increases habitat functional connectivity, which could provide more benefits than increasing the forest area without considering the global connectivity.

KEYWORDS

connectivity metrics, dry forests, Ecuador, forest conservation, fragmentation, functional connectivity, graph theory, land cover change, reforestation, tropical forests

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1 | INTRODUCTION

Deforestation in South America has led to severe habitat fragmentation as a result of the replacement of native forest with an agricultural matrix (Donald & Evans, 2006). Ecuador underwent the highest rate of deforestation of all South American countries during the 90s and the 2000s decades, at rates of -1.5 and -1.8% year⁻¹, respectively (FAO, 2011), and lost 21,340 km² from 1990 to 2020, which is approximately 15% of its remaining forests (FAO, 2020). Seasonal dry forests in particular are undergoing one of highest rates of deforestation in South America, which has led the Ecuadorian dry forest to have a high rate of fragmentation and a poor conservation status (Manchego et al., 2017; Rivas et al., 2021). This makes these forests one of the most critically endangered ecosystems in South America (Ferrer-Paris et al., 2018), which may lead to the collapse of its biodiversity, even in protected areas (Laurance et al., 2012).

The negative impacts of fragmentation on ecosystems signifies that promoting the connectivity in highly fragmented landscapes such as the seasonal dry forest in Ecuador is essential if effective conservation plans are to be designed. In smaller and more isolated habitats, fragments surrounded by a hostile matrix are less likely to maintain their function and the animals and plants that inhabit them to survive, which will have a negative effect on the abundance, distribution, movement and profusion of species and the interaction between them, their reproduction and genetic diversity (Kool et al., 2013;UNEP, 2019).

Connectivity can be defined as the degree to which the landscape facilitates or prevents movement between existing resources (Taylor et al., 1993; Dickson et al., 2019). Connectivity determines a host of ecological functions, including seed and animal dispersal. gene flow and the spread of disturbances. Understanding the flows of matter and energy (Kang et al., 2016) is, therefore, a key aspect as regards the preservation of biodiversity and ecological functions (UNEP, 2015; Hilty et al., 2020). Connectivity is evaluated at the landscape level, at which the reference scale is determined by the use of habitat or the scale of the movement of the targeted species (Tischendorf & Fahrig, 2000). Functional connectivity can be ensured not only when existing habitat units are spatiality contiguous, but also when a permeable matrix or other connecting elements allow the movement of a particular organism among habitat areas that may be distant (Saura et al., 2010) and reflecting observed flow of organisms or genes (Keeley et al., 2021). This is a major concern for the maintenance of wildlife populations, ecological flows and many other landscape functions (Saura & Pascual-Hortal, 2007).

To reverse these high deforestation rates, a National Reforestation Programme was created in Ecuador (Ministerio del Ambiente, 2019) with a cumulative goal of restoration at least 30,000 hectares in three years. Its objective is to reduce gross deforestation by 15% and to restore ecosystems degraded by loss of vegetation cover, mainly in some selected priority areas (Ministerio del Ambiente., 2018). Priority areas allow incentives to be focused on areas where there is a greater likelihood that the greatest results will be achieved and that the efforts invested will

have significant impacts on degraded ecosystems (Ministerio del Ambiente, 2019).

Several studies have shown the usefulness and relevance of the graph theory as regards generating ecological networks and model landscape connectivity (e.g. Sahraoui et al., 2017; Dickson et al., 2019). The graph theory is very useful as regards representing connectivity, with the node being the habitat of the species and the links that connect the nodes representing the potential movement between patches (Rayfield et al., 2011). Here, we propose the application of Graphab software in order to estimate the connectivity of a highly fragmented ecosystem: the seasonal dry forest in the coastal region of Ecuador. This region has the lowest connectivity among natural vegetation in Ecuador owing to fragmentation caused by anthropic activities, and 83% and 14% of its ecosystems have very low and low connectivity, respectively (Rivas et al., 2020). However, there are no detailed studies regarding the evolution of the functional connectivity of the dry forest in Coastal Ecuador. It is, therefore, crucial to consider connectivity as the basis for conservation planning by which to maintain the viability of wild populations, reduce the risk of extinction and increase the stability and integrity (Pascual-Hortal & Saura, 2006) of this highly fragmented ecosystem, which is characterised by a high degree of endemism and some threatened specialist species. The aim of this research is, therefore, to evaluate changes in the structural connectivity of seasonal dry forests between 1990 and 2018, and how this might impact on potential functional connectivity for species groups of different dispersal capabilities. This was done with the following specific objectives: (i) to study deforestation and fragmentation of the Ecuadorian seasonal dry forest during three different periods (1990-2000, 2000-2008, and 2008-2018); (ii) to study its effect on functional connectivity of remnant forest patches using graph theory; and (iii) to compare the current Ecuadorian state's reforestation plan to an alternative reforestation plan informed by graph theory which proposed to maximise connectivity with the smallest reforested area.

2 | MATERIALS AND METHODS

2.1 | Study area

The targeted habitat was the seasonal dry forest in the coastal region of Ecuador (Figure 1). The coastal region of Ecuador is a biographic sector located along the Pacific Ocean and the west slope of the Andes Mountain range (specific location is available at http://ide.ambiente. gob.ec:8080/mapainteractivo/). The entire Ecuadorian coast, plus 10km of buffer area from the Andean region (mountain area), was selected. The coastal region has two clearly differentiable major ecosystems: humid and dry ecosystems (Ministerio del Ambiente del Ecuador, 2013). In the present study, we considered the seasonal dry or deciduous forests (*sensu lato*) of the Ecuadorian Pacific, which include deciduous (*sensu stricto*) and semi-deciduous phenology, in which the dry periods last up to eight months and 25%–75% of tree and shrub species lose their leaves during the dry season (Prentice, 1990;

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FIGURE 1 (a) Map of continental Ecuador showing the location of its three main geographical regions (Coast, Andes and Amazon). (b) The location of the seasonal dry forest (blue) in the study area (coastal region of Ecuador plus 10 km of buffer area from the Andean region, grey).

Rivas et al., 2020). The Ecuadorian coast is included in the Tumbes-Choco-Magdalena biodiversity hotspot (Myers et al., 2000).

The layers of phenology, flooded areas, bioclimate, biogeographic unit and land cover were obtained from the Ecuadorian Ministry of the Environment (available at http://ide.ambiente.gob.ec:8080/ mapainteractivo/). The potential extent of the seasonal dry forests in the coastal region was limited by selecting deciduous and semideciduous phenologies, excluding floodable areas (mangrove areas) and areas of desert bioclimate (these areas are bush or desert). Once the potential dry forest area had been determined (dry forest area; Figure 1b), this layer was overlapped with the land cover layer, and the areas classified as native forest in the latter (in the years 1990, 2000, 2008 and 2018) within the areas of potential dry forest extension were classified as native dry forest. Land cover was obtained by the Ecuadorian Ministry of the Environment, using Landsat satellite images and Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) and orthorectification and these were later certified by experts and by means of fieldwork, with a pixel size of 30 m (Peralvo & Delgado, 2010; MAE and MAGAP, 2015; Ministerio del Ambiente, 2017).

The land cover layers were then converted into raster files with a pixel size of 100 m $\times 100$ m.

Changes in land cover were calculated for the periods 1990-2000, 2000-2008, 2008-2018 and 1990-2018 for the dry forest

area and the entire study area. The original 12 land cover units were then recategorised into six categories: 1, Anthropic zones (populated areas and infrastructures); 2, flooded areas (artificial and natural water bodies); 3, native forests (including humid and dry forests); 4, other natural areas (areas without vegetation cover, forest plantation, shrub and herbaceous vegetation); 5, agricultural land; and 6, areas for which no information was available (Table 1).

2.2 | Fragmentation analysis

Fragmentation was analysed for 1990, 2000, 2008, and 2018, and patches were divided into three categories according to their size $(<1 \text{ km}^2, 1-10 \text{ km}^2 \text{ and } > 10 \text{ km}^2)$ in order to verify trends in the different periods depending on the patch size. Four simple fragmentation metrics were calculated for each category using ArcGIS: the number and proportion of patches for each category, and cumulative areas and proportion of each category.

2.3 | Connectivity analysis

The connectivity metrics between the patches of native dry forest were calculated using the Graphab software (Foltête et al., 2012a).

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Name	Definition	Cost	Reclassified for land cover change as
Native dry forest	Arboreal ecosystem, primary or secondary, regenerated by natural succession; it is characterised by the presence of trees of different native dry forest species, varied ages and sizes, with one or more strata	0	Native forest
Other Native forests	ther Native forests Other arboreal ecosystem except dry forests, primary or secondary, regenerated by natural succession; it is characterised by the presence of trees of different native non-dry forest species, varied ages and sizes, with one or more strata		Native forest
Forest Plantation	Anthropically established tree mass with one or more forest species	1	Other natural areas
Shrub vegetation	Areas with a substantial component of non-tree native woody species. Includes degraded areas in transition to dense canopy coverage and paramo	2	Other natural areas
Herbaceous Vegetation	Areas made up of native herbaceous species with spontaneous growth, which do not receive special care, used for sporadic grazing, wildlife or protection purposes	2	Other natural areas
Natural water	Surface and associated volume of static or moving water	5	Flooded areas
Artificial water	Surface and associated volume of static or moving water associated with anthropic activities and the management of water resources	5	Flooded areas
Populated Area	Areas mainly occupied by homes and buildings intended for communities or public services	10	Anthropic zones
Infrastructure	Civil work regarding transport, communication, agro-industrial and social	10	Anthropic zones
Area without vegetation cover	Areas generally devoid of vegetation, which are not used for agricultural or forestry purposes owing to their edaphic, climatic, topographic or anthropic limitations, but which may have other uses	2	Other natural areas
Agricultural Land	icultural Land Area used for agricultural cultivation and planted pastures, or a rotation between them, including areas of annual crops, semi-permanent crops, permanent crops, grasslands and agricultural mosaic		Agricultural land
No information	This corresponds to areas that it has not been possible to map	5	No information

TABLE 1 Land cover proposed by the Ecuadorian Ministry of the Environment, the assigned cost of moving through them according to Navarro-Cerrillo et al. (2022) and Quimis et al. (2023) and their reclassification for land cover change.

Graphad software works with a raster layer of land cover, in which a certain type of land cover must be designated as "habitat", and the links between habitat patches must then be calculated. Connectivity metrics can subsequently be calculated. This makes it possible to evaluate the loss of global connectivity and to evaluate by zones (patches or components).

The cost assigned to each type of land cover was similar to that calculated by Navarro-Cerrillo et al. (2022) and Quimis et al. (2023) (Table 1). Links between patches of native dry forest were created by means of cumulative cost depending on the land cover (Table 1), with a complete link topology (all the links between patches are potentially taken into account), ignoring links crossing a patch and saving real paths (Clauzel et al., 2019). The links were calculated by means of cumulative cost analyses at three different distances (100, 50 and 5), in which a cost of 1 (each land cover has a different cost; Table 1) and a cell size of 100 m corresponded to 10, 5 and 0.5 km. These distances were selected to consider different species and their different travel distances. For instance, the maximum distance travelled by some reptiles and small mammals could be 0.5 km; the maximum distance travelled by some mediumsize mammal species present in the seasonal dry forests, such as the jaguarondi (*Herpailurus yagouaroundi*), the Ecuadorian whitefronted capuchin (*Cebus aequatorialis*) or the ocelot (*Leopardus pardalis*) (Jack & Campos, 2012; Giordano, 2015; Gonzalez-Borrajo et al., 2017), could be 5 km, whereas 10 km would be the maximum distance travelled by some large species (such as *Puma concolor*) (Gonzalez-Borrajo et al., 2017), thus making it possible to estimate the functional connectivity at larger scales.

The graph was created by employing the non-thresholded graph option (all links between patches are validated, regardless of length). Finally, global metrics, component metrics and patch metrics concerning connectivity (Clauzel et al., 2019; Table 2) were calculated.

An analysis of the links between habitat patches of native dry forest was then carried out, during which their number, their distance in metres and their distance in costs in the years 1990, 2000, 2008, and 2018 at the same three distances were calculated. Once the connectivity analyses had been conducted, components were identified within the study area (Urban & Keitt, 2001): a component

References	Urban and Keitt (2001), Saura and Torné (2009), Foltête et al. (2012b)	Saura et al. (2010)	Saura and Pascual- Hortal (2007)	Urban and Keitt (2001)
 Ecological meaning	The importance of the F metric reflects the importance of the patch network, with higher F metrics showing greater connectivity between patches, thus facilitating the ecological factors that depend on connectivity	EC makes it possible to interpret the dynamics in functional connectivity in relation to the different types of changes in habitat area, and to assess to what extent the gains or losses of the area are actually beneficial or detrimental to maintaining and promoting ecological flows throughout the landscape. Therefore, high values show benefits of maintenance and promotion of ecological flows while low values indicate affected ecological parameters	The probability of connectivity index (PC) is defined as the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected)	A component is a group of connected nodes, signifying that organisms can move (link) between patches (nodes) into the same component, but not into patches of different components and, therefore, cannot communicate with them because they are isolated. This implies that within the same component, there is genetic exchange or other ecological functions on which connectivity depends, but that this exchange does not exist between the different components. A greater number of components shows a landscape with more isolated areas (with fewer ecological flows), while in landscapes with fewer components present less isolation of their populations occurs
deaning	oum of potential dispersion from all patches	square root of the sum of products of capacity of all pairs of patches weighted by their interaction probability	sum of products of capacity of all pairs of patches weighted by their interaction probability, divided by the square of the area of the study zone. This ratio is the equivalent to the probability that two points randomly placed in the study area are connected	Number of components of the graph
Formula	$S\#F = \sum_{j=1}^{n} \sum_{j=1}^{n} a_{j}^{\beta} e^{-ad_{ij}} S_{j\neq i}$	$EC = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j e^{-ad_i}} S$	$PC = \frac{1}{A^2} \sum_{j=1}^n \sum_{j=1}^n a_j a_j e^{-a d_{ij}} S$	Z u u N C
Level	Global level and Component level	Global level	Global level	Global level
Metric	Flux (F)	Equivalent Probability (EC)	Probability of connectivity (PC)	Number of Components (NC)

TABLE 2 Description of connectivity metrics analysed according to Clauzel et al. (2019) and ecological meaning according to bibliographic references.

(Continues)

Metric	Level	Formula	Meaning	Ecological meaning	References
Integral index of connectivity (IIC)	Global level	$ICC = \frac{1}{A^2} \sum_{i=1}^n \sum_{j=1}^n \frac{a_i q_j}{1 + n l_j}$	For the entire graph: product of patch capacities divided by the number of links between them. The sum is then divided by the square of the area of the study zone. IIC is built like the PC index but using the inverse of a topological distance rather than a negative exponential function of the distance based on the link impedance	The IIC index is applicable to any landscape graph, whether fully connected or not, and can assess the importance of maintaining the overall connectivity of any landscape element or combination of landscape elements	Pascual-Hortal and Saura (2006)
Graph diameter (GD)	Global level	$GD = ma_{ij} \times d_{ij}$	Greatest distance between two patches of the graph	In connectivity loss scenarios, two trends occur. The first is an increase in the metric, as patches and connectivity will be lost and this leads to direct paths between distant nodes being lost and replaced by longer stepping-stone paths; in the second trend, as these stepping stones are being lost, a decrease in the metric occurs	Urban and Keitt (2001)
Harary index (H)	Global level	$H = \frac{1}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{1}{n_{ij}}$	Sum of the inverse of the number of links between all pairs of patches	The Harary index increases with increasing connectivity. The Harary index H appears to be an effective index with which to quantify landscape network connectivity in a meaningful manner. In ecological research, the relation between the Harary index and landscape connectivity may be of some significance for a better understanding of ecological processes, such as seed dispersal and gene flow across the landscape	Ricotta et al. (2000)
Connectivity correlation (C _{cor})	Patch level	$C_{Cori} = \frac{ N_i ^2}{\sum_{j \in N_i^{[N_j]}}}$	Ratio between the degree of node <i>i</i> and the degree of its neighbouring patches <i>j</i>	The connectivity correlation metric (C_{co}) examines the relationship between the degree of a node and the degrees of its neighbours. Patches with high C_{cor} values indicate that these patches are highly connected to others, revealing their importance for ecological functions	Minor and Urban (2008), Rayfield et al. (2011)
<i>Note:</i> A, area of the stud <i>j</i> (generally the least-cos	ly zone; a_{C_k} , capacity o :t distance between th moment $k^* \propto b$ hrake of	of component k (sum of the cap tem); e^{-ad_i} , probability of mover provement dictance. R	acity of the patches comprising <i>k</i>); <i>a_i</i> , capacity of pat ment between the patches <i>i</i> and <i>j</i> ; <i>N</i> , number of patch part to weight more or less capacity.	ch i (generally the surface area); d_{jh} distance betwnes; n_c , number of components; N_h , all parches clos	een the patches <i>i</i> and se to the patch <i>i</i> ; <i>n_k</i> ,

TABLE 2 (Continued)

(NC, Table 2) is a group of connected nodes, signifying that organisms can move (link) among patches (nodes) into the same component, and patches of different components cannot, therefore, communicate because they are isolated (Herrera et al., 2017). The number of components and their connectivity (flux metric, Table 2) within the landscape were analysed for the years 1990, 2000, 2008, and 2018 by considering the same distances (100, 50 and 5 km).

The study area was tessellated into 10-km² hexagons, since this is considered to be a more suitable geometry because hexagonal grid interactions are affected by their neighbours, thus making them more acceptable for the modelling of connectivity than square cells (Birch et al., 2017). We selected hexagons of 10km² because 99.8% of the world's forest fragments cover less than 10km² (FAO and PNUMA, 2020). The number of components generated in links of five cost units in the years 1990 and 2018 was counted per hexagon. Only those hexagons containing patches of native dry forest were considered. The hexagons were classified by the number of components (zones without connectivity) in five categories: very high connectivity (1–2 components), high connectivity (3–4 components), medium connectivity (4–7 components), low connectivity and (7–12 components), and very low connectivity (more than 12 components).

The connectivity spatial patterns were described by employing the Getis-Ord Gi*analysis (Ord & Getis, 1995) for the years 1990 and 2018, considering the number of components inside the hexagons. This analysis identifies clusters of high or low functional connectivity (Feng et al., 2018) according to the resulting Z-scores and *p*-values. The *p*-value is a probability value, and *Z*-scores are standard deviations. Regarding pattern analysis tools, there is a probability that the observed spatial pattern has been created by a random process. When the p-value is very small, this means that it is very unlikely (low probability) that the observed spatial pattern is the result of random processes, and the null hypothesis can, therefore, be rejected. Clusters of high Z-values were denominated as hot spots, while those with low values were denominated as cold spots. The results were therefore assigned to seven values for each tile: Cold spot 99% confidence (Z < -2.58; $p \le 0.01$); Cold spot 95% confidence (-2.58 < Z < -1.96; p ≤ 0.05); Cold spot 90% confidence $(-1.96 < Z < 1 - 0.65; p \le 0.1)$; Not Significant (-1.65 < Z < 1.65); Hot spot 99% confidence (Z>2.58; $p \le 0.01$); Hot spot 95% confidence (1.96 < Z < 2.58; $p \le$ 0.05), and Hot spot 90% confidence $(1.65 < Z < 1.96; p \le 0.1)$. Hot spots are clusters where there are many areas without connectivity (many components) and cold spots where there are few components, whereby hot spots will indicate areas of low connectivity and cold spots of high connectivity.

2.4 | Reforestation plans

Two different reforestation plans were evaluated, the first of which was that proposed by the Ecuadorian Ministry of Environment. In this type of land cover, the very high priority reforestation areas proposed by the Ministry of the Environment were added to the 2018 - Applied Vegetation Science 🛸

land cover map (the only ones that the ministry proposes to reforest; Ministerio del Ambiente., 2018).

In this reforestation plan, the definition of priority areas was originated from the integration of two proposed models; the first, which is called biophysical, is related to land use cover for the period 2016, deforestation areas for the period 2014-2016, flows per micro-basin, slopes, fragmentation, vulnerability to climate change, water catchment areas, and the buffer edge effect variable, which is the area to counteract the edge effect. The second (named as socioenvironmental model) concentrates on analysing the population and the economic activities in the territory, and it is related to rural population density, production systems, mining projects, irrigation systems and hydroelectric projects (Ministerio del Ambiente, 2019). As the rural population is the main beneficiary of reforestation, population density was counted as a positive factor (Ministerio del Ambiente, 2018). The union of the two models classifies the reforestation priority areas into four categories: very high, high, medium and low with a percentage of the total of 14%, 43%, 23% and 20% respectively (see Ministerio del Ambiente, 2019).

The second plan was our reforestation proposal plan, which was created by using Graphad to identify areas or stepping stones that would increase the connectivity of the habitat with the lowest possible area. The components generated by the analysis at 10km in 2018 were, therefore, analysed. The link was later measured at a greater distance, and the path of least cost generated between the patches that were previously isolated was analysed. The new patches in these areas were then added in order to eliminate components. Areas of agricultural land, scrub and herbaceous vegetation or areas without vegetation cover were selected as priority locations in which to reforest areas of a size of 100×100 m that could serve to connect areas that were isolated (they were part of different components) in order to unify the continental forest area into a single component. The costs used for the calculation were 100 units, which correspond to 10 km if cost *a* is 1. The same previous connectivity metrics (see above) were calculated for the two different reforestation scenarios.

2.5 | Statistical analysis

Three different generalised linear models were applied in order to test the effect of the year (1990 vs. 2018) and the distance (5, 50 and 100) on the connectivity correlation metric (C_{cor} ; model-1), the distance in metres (model-2), and the cost distance (model-3), which were considered as response variables. The interaction year*distance was also included as an independent variable in the three models, and a negative binomial distribution was used in order to consider over-dispersion data. Finally, post-hoc tests (Fisher LSD) were developed in the linear models to discover any significant differences among the level of the categorical independent variables. All the statistical analyses were carried out using InfoStat software (Di Rienzo et al., 2020).

RESULTS 3

3.1 Land use change

The remaining dry forest area was reduced to 7104 km² in 2018 (represents 25.58% of the potential area), with a loss of 2647 km² between 1990 and 2018, which represents a loss of 9.5% of forest area in 28 years (Figure 2 and Appendix S1).

Between the years 1990-2000, 2000-2008 and 2008-2018, 888.44 km², 916.69 km² and 842.08 km² of forest have been lost respectively, indicating that deforestation is remaining a constant phenomenon (Table 3). The land on which forests had been lost was subsequently put mainly to agricultural use, which increased by 20.11 and 12.96% in the whole study area and in the dry forest area, respectively (Figure 2). However, the land cover with the highest growth in relative terms was that of anthropic land, although it still represented a small surface (<2% of the study area) (Appendix S1).

3.2 **Fragmentation analysis**

The seasonal dry forests studied are becoming more and more fragmented (Table 3, Figure 3), since the number of patches is decreasing, most of these patches are very small, and a significant number of these smaller patches are disappearing ($<1 \text{ km}^2$). Most of the dry forest area was included in a few patches larger than 10 km², which contain more than 80% of the total area. However, they lost 30% of

Land cover change in the dry forest area

their surface between 1990 and 2018, signifying that their average patch size was reduced from 122.71 km² to 93.3 km². Regarding the number of patches, the most frequent were those that were smaller than 1 km², which represents more than 93% of the total number of patches but which covered only 8% of the remaining area in 2018 (Table 3, Figure 3). The total number of patches decreased from 6908 to 5357 between 1990 and 2018.

Between the years 1990 and 2008 there is a trend in the drastic decrease of the number of patches (2569 patches have disappeared), but this trend changes between 2008 and 2018, where the number of patches increases (with 1018 more patches, of which 996 were smaller than 1 km^2) in spite of the loss of area (Table 3).

Connectivity 3.3

Our results show a drastic decrease in functional connectivity metrics (Figure 4), since new components are being formed, that is, zones with no connectivity between them are increasing (and the internal connectivity of components is decreasing) (Figure 4), in addition to which many small patches with low connectivity have been lost. The distance between connected patches is decreasing, harming principally species with a smaller displacement distance (Figure 5).

Some weighted connectivity metrics derived from graph theory deteriorated dramatically during the study period: Appendix S2 shows how global connectivity decreased between 50% and 75% in the most weighted connectivity metrics between 1990 and 2018,



FIGURE 2 Sankey diagram showing the conversion of each reclassified land use in the drv forest area between the years 1990 (left) and 2018 (right). The height of the bars is related to the percentage covered by each land use.

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Year	Category	Number of patches	Area (km²)	Percentage of area (%)	Percentage of patches (%)
1990	<1 km ²	6554	680.33	6.98	94.88
	1-10 km ²	286	726.5	7.45	4.14
	>10 km ²	68	8344.4	85.57	0.98
	Total	6908	9751.23	100	100
2000	<1 km ²	4696	526.9	5.95	93.84
	1-10 km ²	250	679.9	7.67	5.00
	>10 km ²	58	7655.8	86.38	1.16
	Total	5004	8862.7	100	100
2008	<1 km ²	4026	478.2	6.02	92.79
	1–10 km ²	256	730.2	9.19	5.90
	>10 km ²	59	6737.6	84.79	1.36
	Total	4339	7946.10	100	100
2018	<1 km ²	5018	569.1	8.01	93.67
	1-10 km ²	277	750.2	10.56	5.17
	>10 km ²	62	5784.7	81.43	1.16
	Total	5357	7104.02	100.00	100.00

FIGURE 3 Sankey's matrix showing the evolution during the four studied periods of the percentage of dry forest area based on the three categories of patch size. The non-forest area is the percentage of area that has been recovered or lost to forest in areas that have had dry forest for some years. The height of the bars is related to the percentage covered by each land use



while the metrics F, EC, PC and IIC decreased by a respective average of 69.02, 37.95, 61.14 and 65.23%, with these metrics greatly increasing with the distance of the links (Figure 4). This group of metrics decreases less between 2008 and 2018, and even the flux metric increased at all three distances.

The values of the metrics derived from graph topology, such as NC, GD and H, fluctuated over time, but without being strongly influenced by the size of the links. For example, the NC (areas without

connection between them) decreased from 4094 at 0.5 km to 91 at 10 km in 1990. Like the flux metric, the graph topological metrics are up in 2018 compared to 2008.

The connectivity correlation metric (C_{cor}) was lower in 1990 than in 2018 (Model-1; F=34.77; p<0.001; Figure 6) for the three distances considered, since the interaction was not significant (F=2.08; p=0.1252), with lower C_{cor} values at the distance of 0.5 km (F=478.81; p<0.001), and there were no significant differences for 5 and



FIGURE 4 Evolution of connectivity metrics in the years 1990, 2000, 2008, 2018, and in the reforestations plans proposed by the ministry (2018Min) and in the current study (2018Ref) in percentages in the scenarios of links of 0.5, 5 and 10km of cost using the year 1990 as reference value. F, flux; EC, equivalent connectivity equivalent; PC, probability of connectivity; IIC, integral index of connectivity; NC, number of components; H, Harary index; and GD, graph diameter. (a) 5 cost units; (b) 50 cost units; and (c) 100 cost units.

10 km (Figure 5). Dry forests had very few fragments larger than 10 km² (62 in 2018), with high connectivity metric values (Figure 6) and a majority of very small patches (5018, representing more than 8.01% of the dry forest) with connectivity metrics close to zero.

The number of connected patches increased as the distance increased (Appendix S3), but the number of connections decreased over time, since the number of connected patches decreased during the study period. There were 45,354 links in 1990 and 32,060 links



FIGURE 5 (a) Connectivity correlation mean metric (C_{cor}) at the patch level in 1990 and 2018 at the three distances considered (5, 50 and 100 cost units). (b) Distance in metres for the years 1990 and 2018 for the 0.5-, 5- and 10-km links. Error bars represent the standard error of means. (c) Distance in cost for the years 1990 and 2018 for the 0.5-, 5- and 10-km links. Error bars represent standard errors of the means.



FIGURE 6 Connectivity correlation metric (C_{cor}) at the patch level, links and components (black lines) in 2018 at the 5-km level. On the left is the main image of the coast, while numbers 1, 2 and 3 depict enlarged images in order to show more details. The size and colour of the point indicate the value of the metric at the patch level.

in 2018. The median was zero as regards the links of 0.5 km distance in cost, while in the case of 5 and 10km it was close to zero, which was well below average, and the distance in metres also decreased over time (Figure 5).

Regarding the distance in metres, the results of Model-2 showed a significant effect of the year (F = 4840; p < 0.001) and the distance (F=1303; p < 0.001), with higher distance values in 1990 than in

2018 for the three distances. The interaction year*distance was not significant (F = 223; p = 0.215). Similar results were obtained for the cost distance (Model-3), with a significant effect of the year (F = 149; p < 0.001) and the distance (F = 1367; p < 0.001), with higher distance cost values in 1990 than in 2018 for the three distances considered, but with no significant effect of the interaction year*distance (F = 12.3; p = 0.3465).

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Component connectivity decreased between 1990 and 2018 (Figure 7). It should be noted that the zones of maximum connectivity (red) located in the centre (West) and the north of the map decreased their connectivity at cost 5, and at cost 50. At cost 100, the largest component with greater connectivity also underwent slight fragmentation, forming new areas without connectivity in their centres.

The lack of connectivity was observed mainly in the northeast of the study area. This area was that most affected by fragmentation in 1990 and in 2018, and many of the dry forest habitats have now disappeared. The Getis-Ord Gi*analysis showed that the largest areas classified as hot spots in 1990 had partly disappeared in 2018 (Figure 8). Moreover, new areas classified as hot spots of degradation appeared in 2018 in different places in the dry forest area.

3.4 | Reforestation plans

The Ecuadorian Ministry of the Environment has established an area of 653.24 km² with a very high preference for reforestation in the coastal region. Here, we propose the reforestation of only 1.92 km² (with 177 new patches). The ministry's reforestation plan generally has better connectivity metrics than our proposal, and some connectivity metrics (e.g. F, EC, PC and IIC) are improved by between 15% and 10% with respect to the values of 2018 (Figure 4). However, our reforestation proposal has almost no areas in which there is no connectivity in the dry forest of continental Ecuador (Figure 4 and Figure 9), since the number of components (NC) is 8, while the ministry plan has 86, and the graphic size (GD) is 3.5 times higher in our proposal, connecting patches much further apart from each other, thus showing that all current forest fragments with less reforested area could be connected.

4 | DISCUSSION

Deforestation and fragmentation are some of the main threats to forests, which conserve much of the world's biodiversity (FAO and

PNUMA, 2020). Dry forests in America are seriously threatened by increased deforestation (Ferrer-Paris et al., 2018), and the Ecuadorian dry forest is no exception (Rivas et al., 2021). Our results show that the coastal dry forest in Ecuador is undergoing severe deforestation, fragmentation, and loss of connectivity as a consequence of the reduction in the total forest area and the reduction in the number of patches. During the period 1990 to 2018, the dry forests in Ecuador lost 2647 km², which have been transformed into other types of land cover, mostly agricultural, and which has led to the appearance of a large number of habitat fragments and the possibility of passing the threshold of extinction (Arroyo-Rodríguez et al., 2020).

The Ecuadorian coast is very poorly protected, since only 5% of its area is protected by the national protected areas network (Lessmann et al., 2014), and these data become even more critical for the dry forest area (Rivas et al., 2020). Although there are other categories of protected areas, some of them are not preventing deforestation and fragmentation. What is more, some of these protection authorities show that there are higher rates of deforestation and fragmentation than in non-protected areas (Rivas et al., 2021), which have caused many areas of dry forest to disappear (Rivas et al., 2022). The animal groups that would be most threatened by habitat loss, fragmentation and a loss of connectivity would, initially, be those with the greatest home range, such as the Jaguar (Panthera onca) or the Puma (Puma concolor). In fact, these species should be found on the coast region of Ecuador (Brito et al., 2022; IUCN, 2022), but there are almost no recent records of them in the dry forest (Solórzano et al., 2021; Brito et al., 2022), which could indicate that they have become extinct in this region. Furthermore, although species with fewer habitat needs and less range of movement may perhaps suffer less from the afore-mentioned consequences, if this trend continues they will eventually be affected as the result of either fragmentation per se (UNEP, 2019; Hilty et al., 2020) or the loss of connectivity (ecological meaning, Table 2), or may even confront extinction (Semper-Pascual et al., 2018). The situation is aggravated because this area is in the middle of a global biodiversity hotspot (named as Choc/Darien/Western Ecuador) (Myers et al., 2000), stretching from Peru to Panama, and this lack of connectivity could, therefore, divide the hotspots into two non-connected zones with serious



FIGURE 7 Flux metric by components in the years 1990 and 2018 for costs of 5, 50 and 100 in the coastal region of Ecuador. Warmer colours indicate that the component has more connectivity.

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FIGURE 8 Spatial evolution of the connectivity of the equatorial dry forest per tile based on the number of components, and comparison of the hot and cold spots by means of Getis-Ord Gi* analysis in the years 1990 and 2018. The hexagons in the figures on the left were classified by the number of components (zones without connectivity) in five categories: very high connectivity (1–2 components), high connectivity (3–4 components), medium connectivity (4–7 components), low connectivity and (7–12 components), very low connectivity (more than 12 components)



FIGURE 9 Evolution of connectivity with 10-km links for the four studied years and the two reforestation proposals (2018Min=proposed by the Ministry of the Environment; and 2018Ref=proposed by the authors). The habitat patches are shown in dark green, the links in light green and the components (NC) or areas without connection are represented by dark lines.

consequences for biodiversity. Increasing the area of national parks covering the dry forest area should consequently be a conservation priority (Lessmann et al., 2014; van Der Hoek, 2017).

4.1 | Land cover change and fragmentation analysis

This deforestation for conversion into agricultural land is caused by the increase in population at a worldwide level (Laurance et al., 2014; Runyan & Stehm, 2018), and the Ecuadorian population has, in this respect, grown by 550% in only 71 years, reaching 17.5 million inhabitants in 2021 (Villacís Byron, 2012; Instituto Nacional de Estadística de Ecuador, 2022). Moreover, most of Ecuador's agricultural land is located in the Ecuadorian coastal region (Instituto Nacional de Estadística y Censos, 2019), which is probably the main reason why this region has the highest deforestation rate in the country (Sierra, 2013). This increase in population is also reflected in the increase in anthropic lands (such as urban areas), which are those that grow the most in relative terms.

Deforestation is leading to an increase in the fragmentation of the Ecuadorian dry forest (Rivas et al., 2021). In 2018, the number of patches was lower than in 1990, smaller patches had disappeared, and large patches had lost surface. However, between 2008 and 2018 the number of patches increased; this seems to be due to the fact that large patches are losing a higher and higher percentage of area and small parks less and less. In addition, between 2008 and 2018, 5.24% of the forest area was recovered from non-forest to forest, where 28% corresponds to patches of <1 km². In fact, almost

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the same proportion of patches less than 1 km^2 that were lost (1.47%) was recovered (1.74%) (Figure 3).

In this scenario, small patches have been shown to be fundamental in highly fragmented ecosystems (Tulloch et al., 2016; Solórzano et al., 2021). The dry forest has a very small patch size (<1 km²), both globally (FAO and PNUMA, 2020) and in Ecuador (Rivas et al., 2021). These very small patches may be more affected by the edge effect (Hargis et al., 1998), which has serious consequences for biodiversity (Ruffell & Didham, 2016). Many areas of seasonal dry forest have degenerated into savannas, scrublands or grasslands owing to high pressure from livestock and overgrazing (Trejo & Dirzo, 2000; Sales et al., 2020), although there is also a slight conversion of agricultural areas into other natural areas, which could be owing to the abandonment of crops. This would also explain our results concerning the increase in the 'other natural areas' category (which includes areas without vegetation cover, shrub, and herbaceous vegetation).

4.2 | Connectivity analysis

Graphab software has proved to be a powerful tool for connectivity studies, since it allows the analysis of connectivity from various points of view, from the macro (global connectivity) to the micro (patch connectivity), and passing through the intermediate (component connectivity), thus integrating different metrics (Foltête et al., 2012a). Graphab can also be used to identify corridors between patches (Tiang et al., 2021), which would be the links between the patches that are generated by the software. These zones can be selected to protect, reforest, or even eliminate barriers, as occurs when overpasses are constructed over roads. Graphab software, therefore, makes it possible to not only analyse connectivity but also provide relevant information with which to improve it.

Connectivity is, therefore, of vital importance in these highly fragmented ecosystems, and is a key factor for nature conservation (Foltête et al., 2012a). However, dry forests are becoming more poorly connected. This loss of functional connectivity occurs throughout the coastal dry forests in Ecuador, although some areas have lost more connectivity (hotspots) and are, therefore, more vulnerable, and more prone to habitat loss and should be defined as priority areas for protection or reforestation.

In general terms, the connectivity metrics calculated herein decrease over time, since there are fewer areas of forest and fewer patches. The change in land cover leads to an increasingly hostile matrix, thus making connectivity more difficult. The matrix becomes more hostile owing to the increase in land with a higher cost (e.g., agricultural, and anthropic land). Conversely, the increase in distance between different links favours connectivity, since more distant patches can connect or overcome the hostile matrix, thus decreasing their isolation and benefitting species that have longer dispersal ranges (Ray, 2005; Herrera et al., 2017).

Interestingly, between 2008 and 2018 some connectivity metrics (equivalent connectivity, probability of connectivity and integral index of connectivity) did not decrease by the same percentage while some of them even increased (flux, graph diameter, Harary index and number of components) (Figure 4). These results may be due to a significant increase in the number of patches during this period, which could be connecting areas that were not previously connected or maintaining connectivity in areas that are being deforested (Herrera et al., 2017; Siqueira et al., 2021).

Among the calculated metrics, two types of metrics can be distinguished: weighted and topological metrics. Weighted metrics (flux, equivalent connectivity, probability of connectivity and integral index of connectivity) are based on criteria of distance and patch capacity and the topological metrics (Harary index, graph diameter and number of components) are derived from graph theory and do not require adjustment. In our case, since patch capacity is related to area, this explains why these weighted metrics decrease with decreasing forest area (with the exception of flux), but topological metrics depend on graph theory (patches and link), which could explain why they increased as the number of patches increased in 2018 (Table 3). The Harary index, for example, is related to links between all pairs of patches. The new patches created in 2018 are increasing the number of links at distances of 50 and 100 (Figure 4), increasing the Harary and graph diameter metric. Flux, despite being a weighted metric, is strongly influenced by the probability of movement between the patches, so the higher the number of patches, the higher the probability of movement between them [which is why it increases (50 and 100 cost distance) or stays the same (5 cost distance) between 2008 and 2018].

Metrics that do not depend on habitat area and only rely on graph theory (Harary index, graph diameter and number of components) may be good for interpreting ecological factors that depend only on connectivity such as dispersal and migration, the development of population genetic structure and potential responses to climate change (Visconti & Elkin, 2009; Kool et al., 2013), but they alone do not guarantee the viability of populations, as they require a minimum area for their survival or they may not be displaced in the case of an event affecting the viability of the population, such as climate change, inbreeding or natural disasters. In fact low connectivity can lead to extinction even within natural areas (Laurance et al., 2012; Hilty et al., 2020), so it seems essential to connect all areas where large patches can serve as habitats and small patches connect large ones (Arroyo-Rodríguez et al., 2020).

The NC metric fluctuated throughout the study period, probably because it is necessary to consider the analysis of the number of components from a global perspective, since measuring the NC metric in isolation may be misleading. The disappearance of a component could mean an increase in connectivity (by this component being joined to another) (Tiang et al., 2021), or the loss of the forest fragment that contains this component. The first option is owing to an increase in connectivity and the second to an increase in fragmentation (usually indicating a loss of connectivity), while the appearance of a new component may be owing to the loss of connectivity of a forest fragment or to the forestation of an area without connectivity (less fragmentation and greater global connectivity) (Appendix S4). For example, the reforestation plan of the Environment Ministry of Ecuador has a similar NC or areas without connectivity to the dry forest cover in 2018 without reforestation (Figure 4); however, it has more connectivity and more habitat areas because the Environment Ministry of Ecuador proposes to reforest areas that can form a component by not being connected to the existing native forest areas.

Patch to patch connectivity is declining and the links are becoming shorter, mainly owing to three factors: (i) the change in land cover that creates an increasingly hostile matrix, thus making connectivity difficult (Diniz et al., 2020); (ii) the loss of native dry forest, which leads to a loss of habitat and patches, along with other types of forest that imply areas of high connectivity; and also (iii) the fact that large patches are becoming more fragmented (creating new nearby smaller patches) while small distant patches are disappearing (Rivas et al., 2021). It is important to bear in mind that an increase in the number of patches may favourably affect the number of links between patches, along with the fact that even if they are very small, they are very important for connectivity (Tulloch et al., 2016; Siqueira et al., 2021).

The change in land cover towards a more hostile matrix leads to a loss of habitat and connectivity because links get shorter, thus isolating the remaining patches of the ecosystem, affecting biodiversity and reducing species abundance and richness (Sahraoui et al., 2017), which involves a lower genetic exchange (Ricotta et al., 2000). Our results show that other native forests mixed with dry forests play a fundamental role in connectivity, acting as 'corridors' between remote patches or even nearby patches, and do not imply any displacement costs (Figure 9).

The connectivity correlation metric (C_{cor}) examines the relationship between the degree of a node and the degrees of its neighbours (Rayfield et al., 2011). Such areas could, perhaps, be considered priority conservation areas since they are highly connected regions with high forest cover (Minor & Urban, 2008). Our results show that extrapolating the mean of patch metrics as a global connectivity metric is incorrect, since global connectivity decreases, whereas the average connectivity of the patches increases. However, the C_{cor} results could indicate that the large patches are separating and the remote and small patches are disappearing, since the large patches that are divided are still well connected and the remote patches with a low C_{cor} value would be disappearing (Table 3, Figure 5), which would also explain why the average C_{cor} increases.

Upon comparing the images from 1990 and 2018 (Figure 8), it will be noted that many hexagons classified as hotspots in 1990 had completely disappeared by 2018, which indicates where forest fragments may be isolated, with serious consequences for the ecosystem. The analysis makes it possible to identify concretion of forest areas with higher possibilities of becoming isolated, thus allowing to identify the causes and take conservation and/or reforestation measures. This analysis also allows us to identify areas with high or low connectivity, which can also be obtained with the metrics by component. However, as noted in the NC metric, this can increase or decrease indistinctly with greater or less connectivity, and its size is not homogeneous. This does not occur with this analysis, since the hexagons analysed are always the same size and all of them contain forest fragments (hexagons without forest fragments are not considered in the analysis). Nevertheless, there are very large components (NC) in which most of the area is not covered by forests.

4.3 | Ecological consequences of reforestation plans

It has been demonstrated that the reforestation of small areas or stepping stones allows areas without connectivity to be eliminated, thus connecting the entire habitat (Herrera et al., 2017; Arroyo-Rodríguez et al., 2020). When all habitats are connected to form a single very large component, this indicates that no patches are isolated, thus creating a more connected habitat network (Saura & Pascual-Hortal, 2007; Herrera et al., 2017). This type of approach is already being carried out in several countries, as is the case of Nature Network (Ecologische Hoofdstructuur; EHS) in the Netherlands to improve connectivity between existing and new nature reserves that have yet to be created. The network helps prevent the extinction of plants and animals in isolated areas and the loss of natural areas of value.

The Ecuadorian Ministry of the Environment's reforestation programme proposes the reforestation of more surface area than our alternative. However, it has been shown that the number of components or areas without connection is greater than in our proposal, thus demonstrating that small patches or stepping stones are fundamental in connectivity studies (Herrera et al., 2017). According to this theory, areas could be connected in which connectivity has been lost owing to the loss of habitat or for which increased travel costs were selected and small patches were located, and it would, therefore, be possible to connect the entire ecosystem of Western Ecuador. This approach is even an improvement over the previous situation (1990) in which 85 components existed, while only eight components remain in our plans, the majority of which are located on islands. In summary, connectivity is shown to be a priority parameter when reforesting, thus prioritising the connectivity of the entire study area rather than a particular reforested area.

While the Government reforestation plan improves in some metrics the plan proposed by us, these metrics are influenced by the area, so it is logical that these metrics are higher (weighted metrics: flux, equivalent connectivity, probability of connectivity and integral index of connectivity). However, graph diameter and number of components are not influenced by the area and derive only from graph theory and present better results in our plan, and as mentioned in the previous section (see Section 4.2), these metrics can be efficient for interpreting ecological factors that depend only on connectivity such as dispersal and migration, the development of population genetic structure and potential responses to climate change (Visconti & Elkin, 2009; Kool et al., 2013) and that was the objective of our reforestation plan, maintain connectivity throughout the study area, connecting the large habitat patches (Arroyo-Rodríguez et al., 2020). The Harary index, as it depends on the number of connections between the patches, is also improved more in the government reforestation plan, due to the increased number of patches in this proposal.

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Although this approach has several advantages, it also comes with some limitations, since there is not much information on cost evaluation, and even less as regards dry forest animals or Ecuador. The study has addressed this by assigning generic costs to generic species (Hilty et al., 2020), for which a $100 \text{m} \times 100 \text{m}$ raster was used, which can eliminate some patches of smaller forest. Another limitation was the lack of information on the minimum patch size for a patch to be used as a stepping stone, which could affect our reforestation plan. However, a lot of literature states that small patches can be very important and used with this purpose (Herrera et al., 2017; Siqueira et al., 2021; Tiang et al., 2021).

5 | CONCLUSION

According to our results, the Ecuadorian dry forests are affected by fragmentation, deforestation and the loss of connectivity. Our connectivity analysis shows that the other types of forest and other vegetation formations as well as small forest patches are fundamental to global connectivity, since they are used as corridors or natural stepping stones. Many areas run a high risk of disappearing, and it is, therefore, essential to take conservation and reforestation measures, with connectivity being a fundamental parameter to consider, along with prioritising connectivity at the regional scale rather than reforesting a particular area.

The use of connectivity as a key factor has proved important when taking protection, conservation and reforestation measures. This information allows the identification of important patches or areas in the ecosystem's connectivity, areas prone to disappear and lose their connectivity related to reforestation plans. This approach, therefore, enables a better choice of areas that will increase connectivity with the least amount of cost or effort by choosing areas in which to place stepping stones, thus eliminating areas without connectivity.

AUTHOR CONTRIBUTIONS

Carlos A. Rivas: data collection, experimental design, conceptualisation and writing of the original draft. José Guerrero-Casado: statistical analysis, supervision, review and editing of the original draft. Rafael M. Navarro-Cerillo: experimental design, conceptualisation, supervision, review and editing of the original draft. The author(s) have read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

Not applicable.

DATA AVAILABILITY STATEMENT

The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

CODE AVAILABILITY

Graphab software: https://sourcesup.renater.fr/www/graphab/en/ home.html.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Land use change matrices in percentage between 1990 and 2018 in the dry forest area (A) and in the study area (B).

Appendix S2. Evolution of connectivity metrics in the years 1990, 2000, 2008, 2018, 2018 Min (reforestation plan proposed by the ministry) and 2018Ref (reforestation plan proposed in the current study) in the scenarios of links of 0.5, 5 and 10km of Cost.

Appendix S3. Number of links distance in cost and metres.

Appendix S4. Effects of reforestation on the components. Figures A and C correspond to 2018 and Figures B and D correspond to 2018 with reforestations. Figures A and B show how reforestation eliminates components, while Figures C and D show how reforestation creates new components.

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