# The impacts of agricultural and urban land use changes on plant and bird biodiversity in Costa Rica (1986-2014)

Andrea Montero[1], Joan Marull[2], Enric Tello[3], Claudio Cattaneo[4], Francesc Coll[2], Manel Pons[2], Juan Infante-Amate[5], Alexander Urrego-Mesa[3], Alfredo Fernández-Landa[6], Manuel Vargas[7]

[1] University of Costa Rica, 11501-2060 San José, Costa Rica; andrea.monteromora@ucr.ac.cr; +506 25116446; ORCID: 0000-0002-7718-9206

[2] Barcelona Institute of Regional and Metropolitan Studies, Autonomous University of Barcelona, 08193 Bellaterra, Spain; joan.marull@uab.cat, francesc.coll@uab.cat, manel.pons.sanvidal@uab.cat; +34 93 5868880; ORCID: 0000-002-7793-4165/ 0000-0002-3121-6918/ 0000-0002-2072-7288

[3] Department of Economic History and Institutions, University of Barcelona, 08034 Barcelona, Spain; tello@ub.edu, alex.urrego.mesa@ub.edu; +34 93 4021047, +34 93 4035829; ORCID: 0000-0002-4970-1524 / 0000-0002-8256-0321

[4] Department of Economics and Economic History, Faculty of Economics and Business, Autonomous University of Barcelona, 08193 Bellaterra, Spain; claudio.cattaneo@uab.cat; +34 644116328; ORCID: 0000-0002-1836-0210

[5] Department of Economics and Economic History, Faculty of Economics and Business, University of Granada, 18071 Campus of La Cartuja, Granada, Spain; jinfama@ugr.es, +34 958249995; ORCID: 0000-0003-1446-7181

[6] Agresta S. Coop, C/ Duque de Fernán Núñez 2, 28012 Madrid, Spain; afernandez@agresta.org; +34 975215202; ORCID: 0000-0003-4725-8044

[7] Instituto Nacional de Biodiversidad, Santa Rosa de Santo Domingo, 22-3100 Heredia, Costa Rica; mvargas@inbio.ac.cr; +506 25078100

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## 1. Introduction

Agriculture is the human activity that has changed the surface of the Earth the most (Tilman et al. 2002, Phalan et al. 2013). The world crop area reached 15 million km² in 2000 (12% of terrestrial ice-free surface), and pastureland reached 28 million km² (20%; Ramankutty et al. 2008). In the same year agriculture was responsible for 78% of human appropriation of photosynthetic net primary production (*HANPP*), and the other 22% resulted from forestry, infrastructure or human-made fires (Haberl et al. 2007a). Although FAO projections suggest that cropland expansion will represent only 20% of production increases in developing countries, in the coming decades crops will keep growing at the expense of tropical forests (Gibbs et al. 2010). Despite its land-sparing effect compared to more extensive uses, industrial farming also entails deep ecological impacts which include landscape fragmentation, biodiversity loss and ecosystem services disruption (Matson et al. 1997). From 1999 to 2008, cropland took 48,000 km² from tropical forestland annually, while crop yield increases involve the application of fossil-fueled and polluting industrial inputs (Phalan et al. 2013). Together with soybean, corn, sugarcane and oil palm, coffee area also increased, although most Latin American countries mainly focused on improving yields implementing industrial farming through the Green Revolution varieties with high doses of agrochemicals (Patel 2013, Swaminathan and Kesavan 2017, Infante-Amate and Picado 2018).

In a world that faces the dilemma of satisfying the growing demand for food, energy and raw materials, without this causing biodiversity loss (Godfray et al. 2010, Cardinale et al. 2012) the contribution of agricultural landscapes to species diversity is an important topic. Depending on the type of management, farm systems may either decrease or increase biodiversity (Tress et al. 2001, Benton et al. 2003, Swift and van Noordwijk 2004). To reconcile the goals of raising crop production and preserving biodiversity, some experts suggest continuing with the traditional land-sparing approach of increasing agricultural intensification in some areas to devote the land spared to nature conservation and forest transition (Green et al. 2005, Matson and Vitousek 2006). Other scholars propose a land-sharing approach through a wildlife-friendly farming capable of providing complex agroecological landscapes connected with natural sites to jointly maintain high species richness. In this scenario, the agricultural component of landscapes acquires great relevance (Perfecto and Vandermeer 2010, Tscharntke et al. 2012, Marull et al. 2018).

Twenty years ago, Hall et al. (2000) published a sustainability evaluation of Costa Rican economic development during the last decades of the 20$^{th}$ century by combining energy and material flow accounting with GIS assessment of land use and land cover changes, and socioeconomic appraisal. It reported the huge deforestation suffered from 1940 to 1983 that ranked the country fifth in the world in terms of total forest lost, mainly due to the expansion of pastures and extensive cattle ranching driven by the so-called 'hamburger connection' through meat exports to the United States. Deforestation slowed down in the 1980s, and was nearly ceasing in the late 1990s due to the combination of downturn in meat prices, changes in North American and Costa Rican cattle policies, and nature conservation that put up to 29% of Costa Rican territory in 1998 under some degree of protection (Hall et al. 2000).

The actual amount of forest cover lost was in dispute, and the high deforestation figures published by Sader and Joyce (1988) were reexamined by subsequent studies. The comparison between the GIS accounting of aerial photographs and satellite images published by Hall et al. (2000) and later by Algeet-Abarquero et al. (2015) found many scattered fragmented woodlands as well as an increase of secondary forest that began to grow with the retreat of pastures, thus confirming that previous official agricultural censuses had underestimated the non-cultivated land covers (Montero, 2018, Montero, Badia-Miró and Tello 2021). New digital maps reported that in the turn from 20$^{th}$ to the 21$^{st}$ century forestland covered nearly 40% of Costa Rica, although Sanchez-Azofeifa et al. (2001) estimated that mature forest occupied only 29% with a large share of it within National Parks and the central mountains. The difference can be mainly accounted for reforestation processes underway in many, but not all, abandoned pastures. Yet better satellite images also discovered many small remnants of more mature forests that might have been unnoticed in previous studies, an aspect that requires more detailed local and regional studies. In any case, Jadin et al. (2016) clearly confirmed that Costa Rica had stopped past deforestation and a forest transition began during the two first decades of the 21st century. The decline in meat exports caused a contraction of pastures that led to reforestation, later reinforced by other land use reconfigurations driven by agricultural intensification and other changes in foreign trade such as the growing timber imports. According to the last FAO (2020) data, 30% of Costa Rican territory is currently covered by mature forest, 18% by secondary forest, and up to 58% by forestland of all kinds. However, the expansion of agri-food exports continued to cause deforestation in some of the most valuable regions for nature conservation, either directly, occupying former pastures, or to produce pallets for fruit global trade (Jadin et al. 2016).

Hall et al. (2000) also warned about the opposite trends toward nature protection combined with the expansion of new agri-food exports that replaced the retreat of pastures with large monocultures of cash crops in order to cope with the external debt crisis of the 1980s. The agrochemical imports consumed in these plantations of tropical fruits, palm oil and flowers took away a large share of the income gained through exports in the foreign trade balance, and the country's external indebtedness has been perpetuated to date despite several defaults. The advance of the cropping frontier of these agro-industrial commodities counteracted the great efforts Costa Rica made in nature conservation, raising new concerns on how land was unsustainable managed outside national parks isolating them within the land matrix. Reorienting these unsustainable trends requires reforestation programs, soil and water conservation through agroforestry, shade-grown coffee plantations, and other agricultural practices that decrease reliance on industrial fertilizers and pesticides, such as crop diversification and rotations with legumes, intercropping, and biological filters through green fences and other buffer zones (Hall et al. 2000).

In other words, an agroecological change was needed to open a way out of the unsustainable path initiated by trade liberalization after the external debt crisis. Twenty years later, it is time to examine the landscape changes that have taken place in Costa Rica and their impact on how biodiversity is distributed along the gradient of the country's land matrix. Our study provides new empirical results on the land use changes most related to the food-biodiversity dilemma (Chappell and LaValle 2011) and urban growth (Bren d'Amour et al. 2017). We use landscape ecology indicators to study the impact of agricultural systems and metropolitan urban expansion on the location of plant and bird species richness in Costa Rica, in relation to the role of tropical forests and natural parks in this world-class biodiversity hotspot.

## 2. Sources and Methods

### *2.1. Digital land cover maps*

To account for land cover changes through GIS, our landscape ecology study is based on the digital maps of Costa Rica from 1986 to 2014 produced by Fernández-Landa et al. (2016) through an open source software based workflow, as part of the national program on 'Reducing Emissions from Deforestation and Forest Degradation and the Role of Conservation, Sustainable Management of Forests and Enhancement of Forest Carbon Stocks in Developing Countries' (REDD+). They used imagery from Landsat 4 and 5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper (ETM+) and Landsat 8 Operational Land Imager and Thermal InfraRed Sensor (OLI/TIRS) with 30 m resolution. By applying a single trained machine learning algorithm to radiometrically normalized imagery and using iteratively reweighted multivariate alteration detection (IR-MAD) across all maps, they guaranteed the consistency of the land covers identified. We choose three relevant time points (1986, 2001, 2014) of these REDD+ land cover maps, including forests, coffee plantations, permanent crops, annual crops, pastureland, wetlands, urban areas and road networks to assess the landscape ecology impacts on biodiversity of recent agricultural and urban land cover changes.

### *2.2. INBio biodiversity dataset*

The georeferenced landscape ecology indicators obtained from the REDD+ digital maps have been statistically correlated with the locations of biodiversity data currently available in Costa Rica. To achieve that, we used data on the species richness of birds and plants, which are the taxa better represented in the dataset provided by the National Institute of Biodiversity of Costa Rica (INBio) for each cell of a grid of 2.5 x 2.5 km in a set of digital maps based on the current records of the Global Biodiversity Information Infrastructure (GBIF). This dataset has not been compiled using an experimental design of random transects regularly surveyed across the territory. Instead, it is still being compiled by geo-referencing all observations taken from published research and expert communications (https://www.gbif.org/es/). As a result, data coverage is still rather coarse and spatially uneven. To correct for the observation biases contained in the INBio dataset, all 5 x 5 km cells with less than three 2.5 x 2.5 km cells with observations of birds (as they are less represented than plants), and less than four 2.5 x 2.5 km cells with observations of plants (better represented) were discarded, assuming that no comprehensive surveys have been conducted there so far. Accordingly, we reassembled the dataset in a grid of cells of 5 x 5 km that recorded enough 2.5 x 2.5 km sub-cells sampled with this minimum information (Fig.1).

[INSERT HERE FIGURE 1]

Unfortunately, this coarse dataset on plant and bird species richness prevented us from performing statistical analyses at any scale lower than the country-wide level. However, the land cover metrics used in our GIS assessment are more appropriate to be correlated with biodiversity data at the landscape level. This means that the results obtained by correlating them with the bird and plant observations of INBio at the country level should be taken with caution. We started from a statistical analysis of linear regression controlling autocorrelation and multicollinearity of the data. Then we divided the cells by surface and sampling intensity and worked with logarithmic scales to avoid heteroscedasticity.

*2.3. Statistical analysis of farming and urban land use changes on biodiversity conservation*

Given the capacities and limitations of the two main sources previously explained, the REDD+ land cover digitals maps and the InBIO dataset, we performed GIS accounts and statistical analyses to address the research question about the impacts on biodiversity conservation of the land use changes driven by the prevailing agricultural and urban trends during the last twenty years in Costa Rica. First of all, we carried a GIS accounting of the main land covers in 1986, 2001 and 2014 from the REDD+ maps. The REDD+ maps can provide data for limited broad categories of land uses: forest, coffee and other perennial crops, annual herbaceous crops, grasslands, wetlands, tropical *páramo*, bare land

and urban land. This provides a first snapshot of the main land covers of Costa Rica in 1986, 2001 and 2014. In order to know whether the changes observed have been statistically significant we add the results of the two-tailed statistical test assuming equal variances with a significance level of 0.05 and adjusted for all pairwise comparison using Bonferroni tests. However, at this broad scale this snapshot cannot capture finer grain changes such as how these different land covers intermingled with each other and how these landscape configurations changed over time.

To overcome this limitation, we used GIS methods to derive a set of landscape ecology indicators from the REDD+ digital maps as explained in the following subsections. According to the focus of our research, these indicators are aimed at capturing the impacts of human disturbances in landscape gradients affected by farming and urban land use changes either directly (e.g. through tillage, harvesting, etc.) or indirectly (e.g. by the barrier effect that reduces ecological connectivity among forests and nature protected areas). To the values obtained we apply again two-tailed tests, and the marks (*ABC*) appearing under them indicate for each year which ones are statistically significantly different to the other two. From this statistical results we obtain a diagnosis of the main land cover changes experienced throughout this period, focusing on how the heterogeneity, fragmentation and ecological connectivity of the landscapes, combined with the human appropriation of photosynthetic net primary production and the corresponding biomass left available for wildlife, may have impacted the landscape capacity to house biodiversity in Costa Rica.

Based on this evaluation of the change in landscape configurations, we perform an OLS multi-regression analysis that correlates the observations of plant and bird species richness of each 5 x 5 km cell in the InBIO dataset, with the landscape ecology indicators obtained through SIG in the same cells from the REDD+ land cover map of 2014. This second statistical analysis tests to what extent these different landscape attributes can explain the current locations of plant and bird biodiversity in Costa Rica.

Finally, we present the biophysical food trade balance of Costa Rica and the doses of industrial fertilizers applied per hectare from 1961 to 2016, calculated from FAOSTAT data, in order to confirm that the expansion of new export-led tropical monocultures after the Costa Rican external debt crisis of the 1980s, and the urban development of San José metropolis at the expense of traditional shade-grown coffee plantations in the Central Valley, have been two important drivers of the landscape impacts on biodiversity previously evaluated.

### *2.4. IDC modelling approach to evaluate the change in landscape configuration*

Our landscape analysis of Costa Rican land cover changes is focused on how agricultural land use changes are either supplementing (e.g. by providing buffer zones and ecological connectivity) or becoming a barrier for the biodiversity conservation role of forest protected areas together with urban expansion. To that aim, the main set of indicators of landscape configuration used are based on the Marull et al. (2006) Intermediate Disturbance-Complexity model (IDC) to account how the spatial gradients of land cover patterns are affected by different levels of ecology disturbances when farmers alter the photosynthetic Net Primary Production (NPP) and carry out land use changes (Marull et al. 2016). The IDC modelling is based on the theoretical assumption that agricultural landscapes can retain more farm-associated biodiversity when the disturbance exerted by harvesting a share of the photosynthetic Net Primary Production (NPP) is done at intermediate levels through spatiotemporal uneven patterns that allow disturbed species to activate their dispersal abilities and find nearby refuge areas (Loreau et al. 2003, Tscharntke et al. 2005, Marull et al. 2017, 2018). It adopts the landscape continuum model to account for the ecological processes that take place across the land-matrix (Fischer and Lindenmayer 2006), and is based on the interaction of the ecological disturbance exerted by farming (accounted through the Human Appropriation of Net Primary Production, or *HANPP*) together with the landscape patterns (accounted through the Shannon-Wiener Index of land cover diversity and evenness, and other landscape ecology metrics) and ecological processes (accounted through Ecological Connectivity Indices) (Marull et al. 2018, 2019).

Therefore, the IDC model assumes that in farming-disturbed landscapes biodiversity is a complex dynamic outcome of the interaction between the matter-energy left available for other species (calculated with the inverse of *HANPP*) and the landscape patterns and processes that give rise to habitat differentiation. The latter is evaluated, as a first step, by the landscape heterogeneity (calculated with the Shannon Index of land covers) as a pattern that tends to differentiate habitats, provided that the populations of diverse species occupying these habitats are capable to withstand recurrent farming disturbances (such as harvest, tillage, etc.) activating their dispersal abilities to find accessible refuge spaces nearby. This ecological dynamic process requires, in turn, a good ecological connectivity combined with the landscape heterogeneity that keeps habitat differentiation. These combination of landscape patterns (land cover differentiation) and processes (ecological connectivity) is calculated with *Le*, the average between the land cover Shannon Index and the Ecological Connectivity Index (*ECI*) calculated through GIS in the REDD+ digital land cover maps of 1986, 2001 and 2014. Finally, these georeferenced indicators are statically correlated with the INBio dataset of birds and plants recorded in a grid of 5 x 5 km cells across the territory in 2014 in order to test the capacity of those different land cover gradients to house these species richness.

### *2.5. Metrics used to account for landscape patterns and ecological connectivity*

We used GIS methods to calculate from the REDD+ maps the Largest Patch Index (*LPI*) that measures the surface of the largest patch in each sample cell. Similarly, we used these data to apply the Shannon Index (*L*) that accounts for the land-cover equi-diversity (i.e. combining richness and evenness) relying on two components, the number and the proportion of land cover types:

$$L = -\sum_{i=1}^{k} p_i \log_{k+1} p_i$$

where $k$ is the number of different land covers (potential habitats) in each case, and there are $k+1$ possible land covers in each unit of analysis (5 x 5 km sample cells; Fig. 3). Thus, $p_i$ is the proportion of land covers $i$ into every unit of analysis.

We also account for the Ecological Connectivity Index (*ECI*) based on Marull and Mallarach (2005) to account for the capacity of any living being to move in all direction through different land covers which are similar enough to allow such displacement without encountering insurmountable barriers in the landscape. *ECI* relies on defining a set of Ecological Functional Areas (EFA) and a computational model of cost distance of displacement that includes the effect of anthropogenic barriers considering the type of barrier, the range of distances and the kind of land cover involved These EFA determine the surfaces to be preserved to allow hosting diverse species, and to interrelate them through a network of connectors that ensure matter, energy, and information flows. The basic Ecological Connectivity Index (*ECIb*) moves in a normalized range between 0 and 10.

$$ECI_b = 10 – 9\ [ln\ (1 + x_i) / ln\ (1 + x_t\ )^3]$$

where $x_i$ is the value of the sum of the cost distance by pixel and $x_t$ the maximum theoretical cost distance. Then, $ECI_a$ is the absolute Ecological Connectivity Index.

$$ECI_a = \sum_{m=1}^{m=n} ECI_b\ /m$$

where $m$ is the number of EFA considered. $ECI_a$ emphasizes the role all sorts of EFA play in keeping up ecological connectivity. We also calculated the forest basic Ecological Connectivity Index ($ECI_f$) to highlight the role of forestland of all kinds as providers of ecological connectivity.

### *2.6. Using IDC metrics to account for agricultural landscape impact*

In order to assess the capacity of different land covers and levels of farming disturbance to house the biodiversity of plants and birds recorded by the INBio dataset, we combined in the Intermediate Disturbance-Complexity Index different metrics commonly used in Landscape Ecology aimed to account for the positive impacts of land cover diversity (Shannon Index) on habitat differentiation, and the negative impacts of fragmentation (Larger Patch Index). The IDC indicator combines the inverse of the Human Appropriation of Net Primary Production (i.e. the photosynthetic NPP left free for non-domesticated species) with landscape heterogeneity and ecological connectivity indicators assuming that the interplay between farmers' patch disturbance and landscape complexity (land cover heterogeneity–connectivity) is a key mechanism for biodiversity maintenance in human-transformed landscapes.

Following Marull et al. (2015), we obtain *Le* as an indicator of Landscape Complexity, aimed at jointly capturing landscape patterns (*L*, heterogeneity) and processes (*ECI*, connectivity).

$$Le = \frac{\left(L + \frac{ECIa}{10}\right)}{2}$$

Then, we use *HANPP* as an indicator of anthropogenic disturbance (Marull et al. 2016). To assess farming-induced pressures on biodiversity, *HANPP* measures the combined effect of harvest and land conversion on the biomass flows that remain available for wildlife in terrestrial ecosystems (Haberl et al. 2007b, Krausmann et al. 2009). It is calculated according to (Haberl et al. 2014):

$$HANPP = NPP_{luc} + NPP_{harv} \; ; \; NPP_{luc} = NPP_0 - NPP_{act}$$

where $NPP_{harv}$ is the NPP appropriation through harvest, and $NPP_{luc}$ is the change of *NPP* through land conversions. $NPP_{luc}$ is the difference between the *NPP* of the potential ($NPP_0$) and actual ($NPP_{act}$) vegetation. $HANPP$ values are assessed in each land cover of the study area, and the fixed coefficient ($w_i$) associated to each land cover *i* is multiplied by the surface it occupies in each cell accounted.

$$HANPP = \sum_{i=1}^{k} w_i p_i$$

where $w_i$ denotes the farming-induced impact of land-cover $i$, and $p_i$ the proportion of land cover $i$ in the cell. Variations in HANPP depend on not only the variations of $p$, but on the variations of $w$ as well.

*HANPP* values have been estimated after assessing different photosynthetic *NPP* and harvested amounts per land cover. $NPP_0$ has been derived for Costa Rica in 1986, 2001 and 2014 from the series of georeferenced annual global data provided by the GIS dataset of the Institute of Social Ecology at the Vienna University of Natural Resources and Life Sciences (Krausmann et al. 2013, available at http://www.uni-klu.ac.at/socec/inhalt/5605.htm). $NPP_{act}$ values have been estimated as the sum of harvested and unharvested values, after performing a literature review on *NPP* by tropical crops (Marull et al. 2017). Harvest ratios from each land-cover across the time points have been transformed into energy values using the conversion factors and the unharvested biomass ratios given in Guzmán et al. (2014).

Finally, the *IDC* indicator combines the landscape complexity indicator (*Le*) with the biomass that remains available for non-domesticated species after the *HANPP*:

$$IDC = Le * E = Le\,(1 - \frac{HANPP}{100})$$

where $E$ is the energy flow available for wildlife food chains, and $Le$ evaluates the landscape heterogeneity and ecological connectivity, which together give rise to complex and well-connected landscapes.

This set of land cover composition and configuration metrics and the IDC modelling is used to estimate the impact of land cover changes (1986-2001-2014) on the capacity of the different landscape gradients to maintain ecological processes and biodiversity in Costa Rica.

## 3. Results and discussion

### *3.1. Landscape ecological assessment of land cover changes*

According to the land cover changes and landscape ecology indicators we have obtained through GIS from the new digital maps provided by the REDD + (Fernández-Landa et al. 2016), in Costa Rica the land-matrix remained dominated by tropical forestlands, which during the years 1986-2014 covered 58-60% of the territory. Together with grasslands and *páramo*, uncultivated and non-urbanized land covers occupied up 83-84% (Fig. 2 and Table 1). These results confirm the forest transition path toward reforestation followed by Costa Rica since the beginning of the 21st century (Fernández-Landa et al. 2016, Jadin et al. 2016, FAO 2020).

[INSERT HERE FIGURE 2 AND TABLE 1]

To this general snapshot shown in Table 1, the only statistically significant changes added by the two-tailed tests performed (see the *ABC* marks under each value) is the highest proportion of urban land in 2014 compared to 2001 and 1986, and the smallest area of coffee plantations in 2014 compared to 1986 and 2001. This clearly highlights the urban sprawl of the metropolis of San José at the expense of the old coffee plantations in the Central Valley (Montero, 2018; Montero, Badia-Miró and Tello, 2021). Urban land experienced a twofold increase from 0.45% in 1986 to 0.9% of the territory in 2014, while the area under coffee plantations contracted 29%, covering from 2% in 1986 to 1.4% in 2014. Despite the expansion of coffee plantations to other regions, a relevant share of them remained concentrated around the crop belt of the metropolitan area in the Central Valley together with basic grains and vegetables (Fig. 3).

[INSERT HERE FIGURE 3]

Urban-industrial expansion went hand in hand with the spread of linear transport infrastructures, mainly based on road traffic, which exert a strong barrier effect fragmenting and tending to isolate nature protected areas one another and with the rest of land covers. The intense impact of urban sprawl in the metropolitan fringes of San José can be shown in the greater decreases of the Ecological Connectivity Index (1986-2014) in forestland $\left(ECI_f\right)$ compared to the connectivity indices in the whole land-matrix $(ECI_a)$ of the Central Valley (Fig. 4).

[INSERT HERE FIGURE 4]

The general trend observed in land cover configuration at country level does not exclude the possibility that deforestation would prevail locally in some valuable ecological areas where new export crops have been expanded, as Jadin et al. (2016) point out, and the existence of other environmentally detrimental land use changes between and outside forest areas such as greater landscape fragmentation and lower ecological connectivity. Deepening the analysis requires taking into account how these broad categories of land cover considered so far became intermingled or rather isolated from each other, giving rise to different landscape gradients throughout the territory. The results of our evaluation of this landscape configuration through landscape ecology indicators show statistically significant increases in the *HANPP* values in farmland, and also statistically significant decreases in both the *IDC* and the Ecological Connectivity Indices either in forestland or across the whole land-matrix (Table 2) which point out to the impact of industrial monocultures.

[INSERT HERE TABLE 2]

While Shannon Land Cover Diversity Index (*L*) does not show statistically significant changes over the period considered, confirming the IDC modelling assumption on the need to combine this with other indicators, both Absolute Ecological Connectivity Index ($ECI_a$) and Ecological Connectivity Index in forestland ($ECI_f$) were higher and significatively different in 1986 than in 2001 and 2014 (see the *ABC* marks under each category). Landscape Ecology metric (*Le*) and Intermediate Disturbance-Complexity (*IDC*) were higher and also significatively different in 1986 and 2001 than in 2014. And Human appropriation of NPP (*HANPP*) was higher and significatively different as well in 2014 than in 2001 and 1986.

All these statistically significant results related to changes of landscape configurations confirm that the reduction of pastures and the beginning of a forest transition, thanks to natural parks and the net gains from reforestation, were accompanied by a decrease in ecological connectivity through the land matrix, and even within forests due to their increasing fragmentation and interposition of barriers that isolate them experienced from 1986 to 2001. *HANPP* data also confirm the statistically significant negative ecological impact of highly intensive farming of industrial export crops, that became one of these ecologically disturbing barriers. At the country level, ecological connectivity in forestland ($ECI_f$) diminished 2% from 1986 to 2001, and then maintained the same level up to 2014. The absolute ecological connectivity ($ECI_a$) experienced instead a significant 13% reduction throughout the period, in this case mainly due to the impact of export monocultures that expanded at the expense of pastures preventing further increases in forestland (Figs. 5 and 6).

[INSERT HERE FIGURES 5 AND 6]

In order to assess the impacts of these land cover changes on the capacity of landscape gradients to house biodiversity, we carried out Ordinary Least Squares (OLS) regressions of the capacity of our indicators of land cover composition and landscape configuration to explain the location of plants and bird species richness in the INBio data available in the same cells of 5 x 5 km.

[INSERT HERE TABLE 3]

Table 3 shows all the OLS results statistically significant at 0.1 and 0.05 levels. Forestland covers appear positively correlated with the richness of birds and plant species, and also wetlands for plants but not for birds (a surprising result due to the coarse grid of cells we have had to use with the INBio dataset). The significant negative sign of the harvested amounts removed from the NPP per hectare ($NPP_h/ha$) clearly denotes the disruptive effect of industrial monocultures on bird species richness. Taken separately, both landscape complexity (ln_*Le*) and Largest Patch Index (ln_*LPI*) appear negatively correlated with plant and bird species richness, again due to the weight of industrial monocultures as well as urban land that make them to capture their detrimental impacts on landscape fragmentation and ecological connectivity. However, when both indicators are combined in the same land covers within each cell (ln_*LPI_Le*), their interaction becomes positively correlated with the species richness of plants and birds. That captures the positive effect on biodiversity when land cover diversity avoids landscape fragmentation giving rise to large patches with a well-connected land cover heterogeneity capable to house more differentiated habitats.

### *3.2. Physical trade balances as drivers of land cover change*

Finally, we calculated the evolution of the physical trade balance of Costa Rica from 1961 to 2016 in order to relate our evaluation of these landscape changes assessed by means of landscape ecology indicators with the main driver of the unsustainable development path of Costa Rica put on the forefront by Hall et al. (2000) twenty years ago, namely the structural adjustment imposed by the International Monetary Fund and the World Bank to secure the loans needed to cope with the country's external debt (Fig. 7).

[INSERT HERE FIGURE 7]

It is apparent that in order to obtain sufficient foreign exchange after the debt crisis of the 1980s, Costa Rica has rapidly expanded old and new export crops, such as bananas, pineapples and other fruits, oil palm, sugar and vegetables, while maintaining the traditional coffee exportation. This has been done jeopardizing the country's food security, which has become dependent on increasing imports of cereals, legumes, meat and even wood products. Measuring this trade deficit in biophysical terms helps to highlight that the growing millions of tons exported involved greater biomass exits whose energy and nutrient content was lost as a necessary organic matter resource for the terrestrial ecosystems of Costa Rica, either aboveground or belowground. Conversely, most of the soil nutrients contained in the tons of imported food were also lost through the wastewater after having fed an increasing part of the country's human population concentrated in the metropolis of San José. The resulting wider gap in organic matter that is not replenished into the soil has been filled by increased imports of industrial fertilizers (Fig. 8).

[INSERT HERE FIGURE 8]

Synthetic or mineral fertilizers supply nutrients only to the crops grown to be exported, not to the whole soil biota such as organic matter does. Along with fewer hours of sunlight per day, soil nutrient storage is one of the most limiting resource in tropical lands subject to strong water erosion and leaching, meaning that the greatest return on investment in agriculture would be from those practices which enhance soil and water conservation (Hall et al. 2000). Agroforestry is the best way to do it, by restoring and retaining soil organic matter in the tropics (Palm et al. 2001, Montagnini 2018). Our results show that almost no agroecology change has been implemented, contrary to what was recommended twenty years ago (Hall et al. 2000).

The only partial exception has been those coffee plantations that retained or increased different shade-grown patterns (Fig. 9) with leguminous trees so as to provide organic N to the soil and lower the respiration rates of coffee plants to allow them to use less energy for their maintenance and increase the net primary productivity of the whole agroforestry system (Beer et al 1997, Hall et al. 2000: 602-605, Charbonnier et al. 2017). From the 1960s to the 1980s there had been a replacement of traditional shade trees by more commercial species, or none, under the strong political and market pressures to embrace the Green Revolution types of farm management (Perfecto et al., 2005). That led Costa Rican farmers to attain the worldwide record yields of nearly 1,700 kg/ha in 1984-85 (Montero 2018: 127, Sfez 1995, 2000, Samper 2001, Lopez and Picado 2012). However, from the 1986 onwards average yields went down again to some 900 kg/ha in 2008, comparable to the ones in 1967 (Montero, Badia-Miró and Tello 2020). The high cost of the agrochemicals imported under the trade openness led many small family growers to try to reduce their dependence on external industrial inputs (Infante-Amate and Picado, 2018) by partially recovering the former biocultural heritage of shading coffee plantations with leguminous tress (Hall 1976, Samper 2001, 2010). 74% of coffee area was under shade in 1992, and the most common tree was *Erythrina poeppigiana* (Obando 1995: 5, De Melo 2005, De Melo and Monge 2008, Campbell 2012, Rojas et al. 2012, Rapidel et al. 2015). In 2008 there were more than 262 different tree and shrub species in coffee plantations in the Central Valley (Virgilio Filho 2008). The return to shaded coffee-growing practices preceded the Payment for Ecosystem Services implemented in 1996, and was reinforced by them (Sequeira 1991, MAG 1992, 1994) as well as by the growing number of hectares under the Rain Forest Alliance (26% in 2015) or fair trade (31%) seals (Montero 2018: 198-200).

### *3.3. Impact of land cover change on biodiversity*

Our maps, landscape ecology indicators and statistical results clearly confirm two main facts. On the one hand, the forest transition started in the turn to the 21st century as well as the role these growing tropical forests play to maintain species richness –here evaluated using plants and birds in the INBio dataset as proxy— in a Central American nation that is a biodiversity hotspot of utmost global importance. The digital map of ecological connectivity in forestland ($ECI_f$, Fig. 5) emphasizes that those tropical forests constitute the actual land matrix of Costa Rica where all the other land uses are interspersed. Although the average ecological connectivity values within forestland ($ECI_f$) slightly diminished 2% from 1986 to 2001, it remained at a stable high level up to 2014. This side of the issue supports the successful outcome of the Natural Parks mainly created in different types of tropical forest, and some wetlands, by the Costa Rican conservation policy following a land-sparing approach to date.

On the other hand, our results point to the ecological detrimental impact of the two most relevant land use changes carried out outside forests from 1986 to 2014 in Costa Rica, as evaluated with the significant negative sign of the correlation with bird observations of the biomass NPP harvested through farming, and also with the negative signs of the largest patch ($LPI$) and landscape diversity ($L_e$) indices when taken separately to be correlated with plant and bird data. These land cover changes have been: 1) the expansion of industrial crop monocultures –such as palm oil along the Pacific

Regions, pineapple and banana in the Caribbean Regions, rice in the plain of the Tempisque River in Northwestern Guanacaste Region, among others—, mainly at the expense of former pastureland; and 2) the metropolitan urban sprawl carried out at the expense of former coffee plantations in the Central Valley, which led to a particularly sharp decrease in the ecological connectivity of forestland in this area ($ECI_f$, Figs. 3 and 4).

The combined effect of industrial farming and urban sprawl resulted in a 13% reduction in the average values of absolute ecological connectivity ($ECI_a$, Fig. 6) across the Costa Rican territory. The main drivers were the landscape fragmentation and the barrier effect following the expansion of both export monocrops and urban-industrial infrastructures, which tended to isolate the Costa Rican nature protected sites and other forestland areas each other. This confirms the concerns on what was happening outside forests and natural protected sites and point out to the need to lessen the negative environmental impacts of agro-industrial farming. But under the pressure to cope with the external debt crisis the country went in the opposite direction, as shown by the evolution of the biophysical trade balance and consumption of industrial fertilizers. While the granting of an innovative scheme of public Payment for Ecosystem Services (PES) in 1996 seems to have helped private reforestation initiatives, and also a greater agroforestry management of shaded coffee plantations, it failed to date as a means to foster an agroecology change toward true wildlife-friendly ways of farming following a land-sharing approach to nature conservation (FAO 2018; Altieri and Nicholls 2012).

Costa Rican population growth was 2.59% per year in 1995 and diminished to 0.96% in 2019. However, the economic structural change from the primary to secondary and tertiary sectors induced a fast rural-urban migration. Urban population grew from 44.5% in 1984 to 77.6% in 2014, and urban area doubled in the last three decades. These trends were not steered by an adequate land use planning aimed at keeping the green belt of coffee plantations and other crops surrounding the metropolitan area of San José. Instead of enhancing its buffer role as a green infrastructure in the Central Valley, the increasing abandonment turned many coffee plantations located in the urban-rural fringe into the typical urban fallow waiting for new land urban developments. Many researches confirm that heterogeneous shade-grown coffee agroforestry contributes to biodiversity maintenance for birds (Hernández et al. 2013), beetles, bees, butterflies and other insects (Rojas et al. 1999, Sánchez et al. 2014), mammals (Granados et al 2008, Caudill et al. 2015) and plants (Perfecto et al. 1996, 2003, Moguel and Toledo 1999, Somarriba et al. 2004, Komar 2006, Vandermeer and Perfecto 2007, Perfecto and Vandermeer 2008, Méndez et al. 2010, Philpott and Bichier 2012, Perfecto et al. 2014, Coral-Acosta and Pérez-Torres 2017, Smith et al. 2018). Yet these researches have so far been conducted on a plot or farm scale. Unfortunately, our statistical results obtained with the INBio dataset using landscape ecology indicators at the country level have failed to ascertain any positive impact of coffee plantations on bird and plant locations at country-wide level. This unexpected result seems to involve a recognition of the limits of the landscape indicators used, of the biodiversity data currently recorded in the INBio dataset, of the coarse grid of cells applied on a national scale, or of all these methodological factors taken altogether. More research is needed on this important issue.

Even though, this study has been able to test a significant correlation with plant and bird biodiversity of those cells that combine heterogeneous land covers with high ecological connectivity and avoid fragmentation by keeping a large patch index (ln_*LPI_Le* in Table 3) across the Costa Rican territory. This can be interpreted as an opportunity to counter the isolation of forest National Parks with agroecology corridors connecting them in line with the FAO's Scaling Up Agroecology strategy (FAO 2018; Altieri and Nicholls 2012), and deserves a further study focused on a lower scale to discover where those landscape patches outside of National Parks are currently located and what they look like. Since the early 1990s, Costa Rica implemented the establishment of biological corridors as a strategy for seeking connectivity among protected areas. During the past years, forty new biological corridors have been established to connect National Parks, but there is no research evaluating their functionality as connectivity spaces (Morera-Beita et al. 2021).

## 4. Conclusion

Costa Rica, a small country that hosts almost 4% of the Earth's biodiversity, is recognized worldwide for its nature conservation policy, reforestation campaigns, ecotourism and pioneering implementation of payment for ecosystems services (Sánchez-Azofeifa et al. 2001, Kohlmann 2011, Obando 2013). Until recently, this nature conservation policies have focused on the establishment of protected areas following the traditional land-sparing approach. According to our results, these conservation policies have been very successful in stopping and reversing previous worrying deforestation and in preserving a large forest land matrix where most of the species richness of birds and plants currently recorded in the INBio dataset is located.

However, our results also confirm concerns raised previously by Hall et al. (2000) and Jadin et al. (2016) on the detrimental environmental trends driven by the expansion of export monocultures in agricultural land, and the unplanned urban sprawl in San José metropolitan area, which are jointly fragmenting and isolating the tropical forests preserved in Natural Parks. In 2009 the payment for ecosystems services were extended to coffee agroforestry (Berbés et al. 2017, Sánchez and Navarrete 2017, Barrios et al. 2018), meaning a new societal recognition that agroforestry can improve landscape ecological connectivity and reinforce the role of tropical forests in biodiversity conservation (Montagnini et al. 2015, Montagnini 2018). Yet at the same time, Costa Rica went through a reduction in the area of coffee planted mostly in the same Central Valley where urban sprawl creates a growing barrier effect among forest protected areas.

We suggest that overcoming these negative trends would require more sustainable farming and agricultural landscapes. Costa Rican scientists and authorities are aware of that, as shown by the approval in 2009 of the new executive decree 33101-MINAE encouraging the National Program of Biological Corridors to improve ecological connectivity (Boraschi 2009, Barquero and Hernández 2015, González 2017, Moran et al. 2019, Morera-Beita et al. 2021). Unfortunately, our results also show that until 2014 these attempts have not yet succeeded to halt the loss of landscape ecological connectivity. They point to the need for two main efforts following a land-sharing approach to nature conservation: 1) a new land use planning for the central metropolis that preserves the remaining green belt of the shade coffee plantations as a green infrastructure; and 2) a change toward organic agriculture and agroecological landscapes, not only in agroforestry coffee plantations but in all of Costa Rican agriculture.

**Table 1** Changes in land cover composition (percentage, 1986-2014) in the Costa Rica's 5 x 5 km sample cells and their statistical significance according to two-tailed tests (*ABC*)

| Land cover composition | 1986 (A) | 2001 (B) | 2014 (C) |
|---|---|---|---|
| Forestland | 61.18 | 59.01 | 60.21 |
| | – | – | – |
| Coffee | 2.15 | 2.56 | 1.52 |
| | *C* | *C* | – |
| Perennial crops | 5.01 | 5.16 | 5.43 |
| | – | – | – |
| Annual crops | 3.34 | 3.60 | 3.50 |
| | – | – | – |
| Grasslands | 24.36 | 25.41 | 24.45 |
| | – | – | – |
| Wetlands | 2.51 | 2.28 | 2.31 |
| | – | – | – |
| *Páramo* | 0.23 | 0.23 | 0.23 |
| | – | – | – |
| Bare land | 0.56 | 0.70 | 1.08 |
| | – | – | A B |
| Urban | 0.46 | 0.78 | 0.94 |
| | – | – | *A* |

The results are based on two-tailed test assuming equal variances with a significance level of 0.05. For each significant pair, the key under the category (ABC) shows up beneath the category with a major average value. They have been adjusted for all pairwise comparison using Bonferroni tests.

**Table 2** Changes in landscape configuration (1986-2014) and their statistical significance according to two-tailed tests (*ABC*)

| Landscape configuration | 1986 (A) | 2001 (B) | 2014 (C) |
|---|---|---|---|
| Shannon Land Cover Diversity Index (*L*) | 0.26 | 0.27 | 0.27 |
| | – | – | – |
| Absolute Ecological Connectivity Index $ECI_a$ | 3.46 | 3.31 | 3.01 |
| | *B C* | *C* | – |
| Ecological Connectivity Index in forestland $ECI_f$ | 8.36 | 8.16 | 8.16 |
| | *B C* | – | – |
| Landscape Ecology metric (*Le*) | 0.30 | 0.30 | 0.28 |
| | *C* | *C* | – |
| Human appropriation of NPP (*HANPP*) | 0.49 | 0.48 | 0.50 |
| | – | – | A B |
| Intermediate Disturbance-Complexity (*IDC*) | 0.15 | 0.15 | 0.14 |
| | *C* | *C* | – |

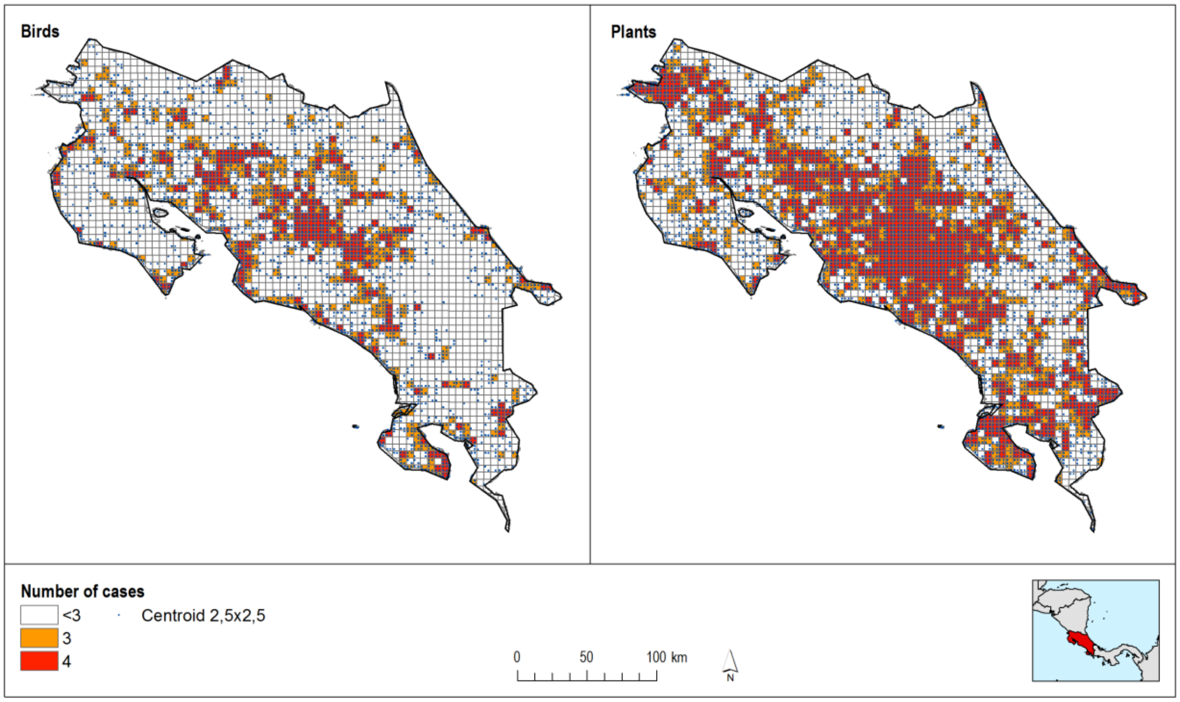
The ABC results are based on two-tailed test assuming equal variances with a significance level of 0.05. For each significant pair, the key under the category (ABC) shows up beneath the category with a major average value. They have been adjusted for all pairwise comparison using Bonferroni tests.

**Table 3** OLS regression of Intermediate Complexity Disturbance (IDC) and landscape ecology variables on the INBio data of birds and plants in the Costa Rica's 5 x 5 km sample cells in 2014

| | Model for birds | Model for plants |
|---|---|---|
| Constant | 2.188<br>(0.161) | -1.992<br>(0.670) |
| Forest | 0.155<br>(0.018) | 0.433 |
| $NPP_{harv}$/ha | -0.001<br>(0.000) | - |
| ln_*LPI* | -0.388<br>(0.000) | -0.115<br>(0.682) |
| ln_*Le* | -6.576<br>(0.000) | -7.300<br>(0.023) |
| ln_*LPI*_·_*Le* | 0.370<br>(0.000) | 0.418<br>(0.029) |
| Wetlands | - | 0.450<br>(0.083) |
| N | 551 | 319 |
| adj. $R^2$ | 0.631 | 0.132 |
| F | 188.898 | 10.681 |
| p-value (F) | 0.000 | 0.000 |

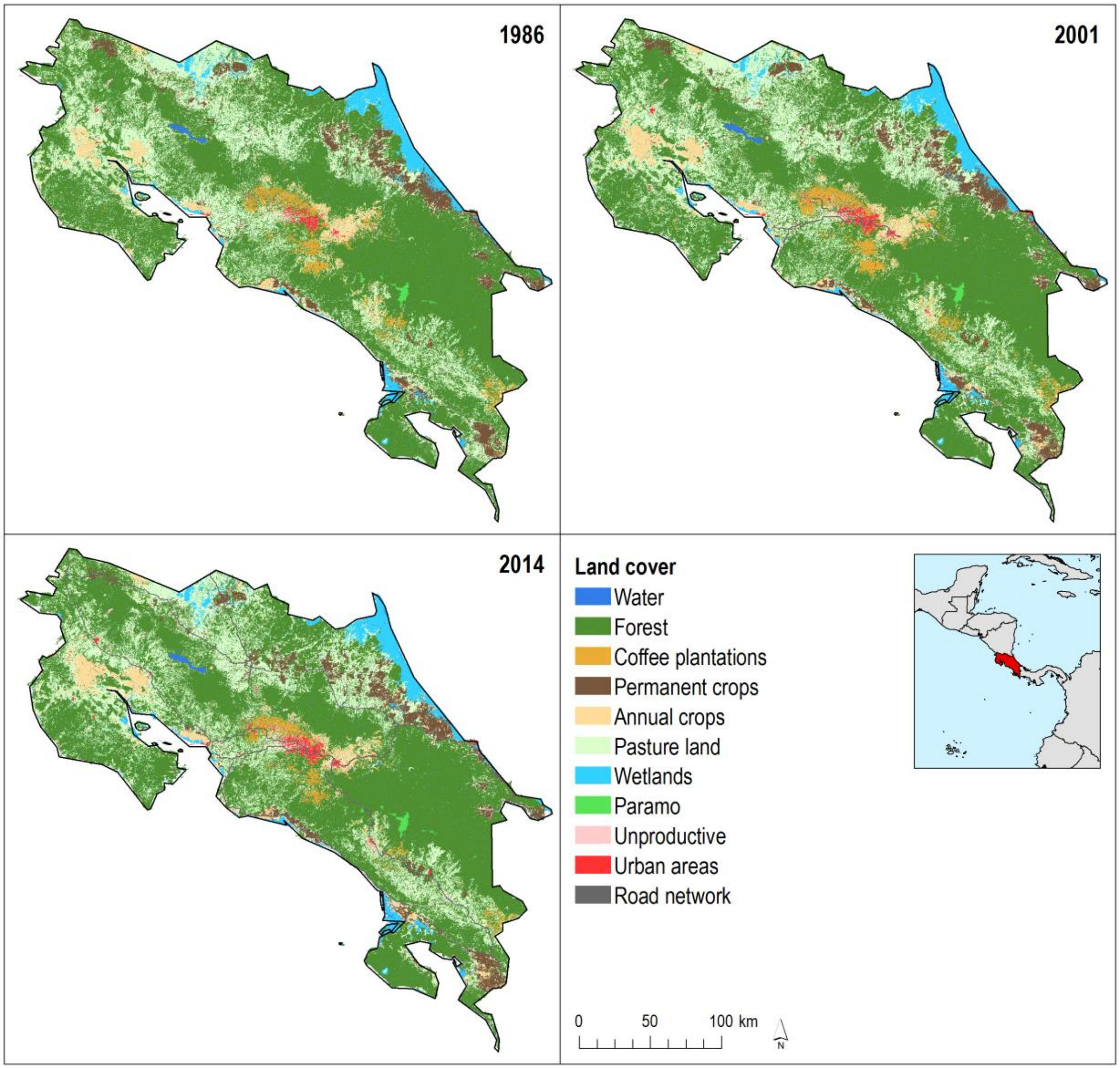
OLS (ordinary least squares) regressions. The values presented are estimated coefficients; significance p-values are in parenthesis below the coefficients. Significances levels of 0.05 and 0.1. The dependents variables are, respectively, naperian logarithm of number of birds/ha and naperian logarithm of number of plants/ha. In both variables, previously, a Kolmogorov-Smirnov normality test was performed. There is no multicollinearity between the regression variables as all VIF values are between 1.32 and 2.39 (except the interactions variables ln_*LPI*, ln_*Le*, ln_*LPI_Le*) in both regression models. *Le*: Landscape Complexity; *LPI*: Largest Path Index; $NPP_{harv}$: Net Primary Production harvested.

**Fig. 1** Maps of the INBio registers of birds and plant species in Costa Rica (5 x 5 km sample cells)



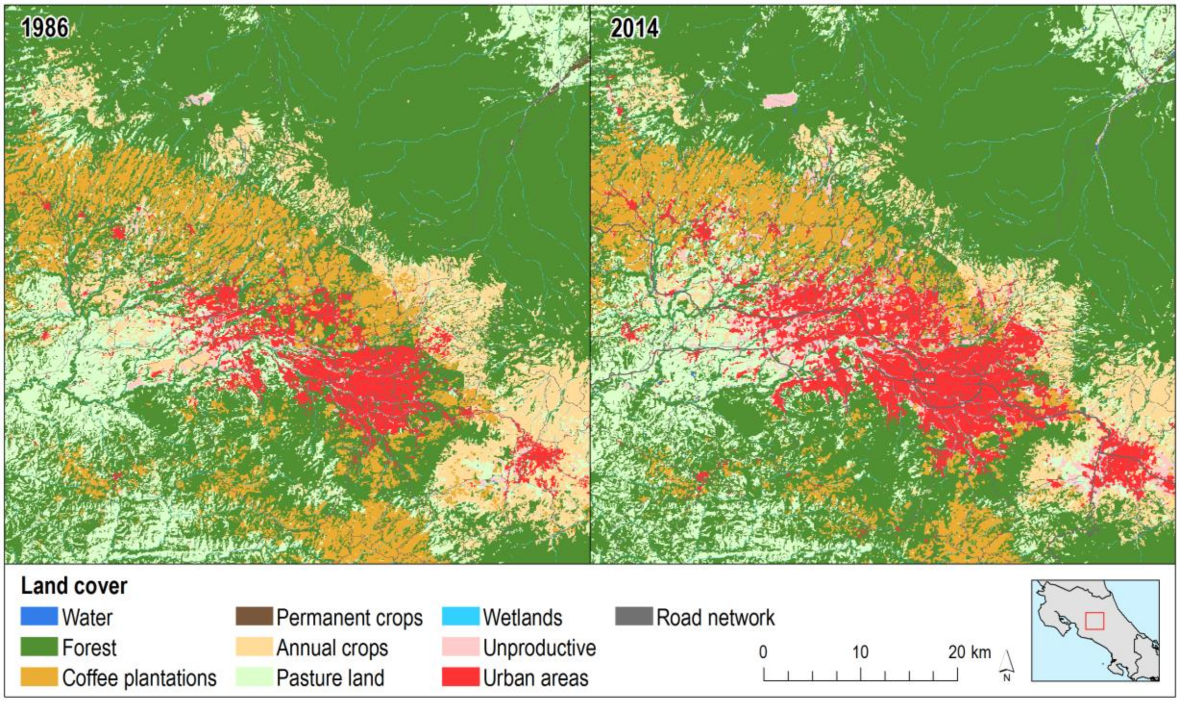

Source: Own elaboration from the INBio dataset

**Fig. 2** Land Cover Changes in Costa Rica (1986, 2001 and 2014)



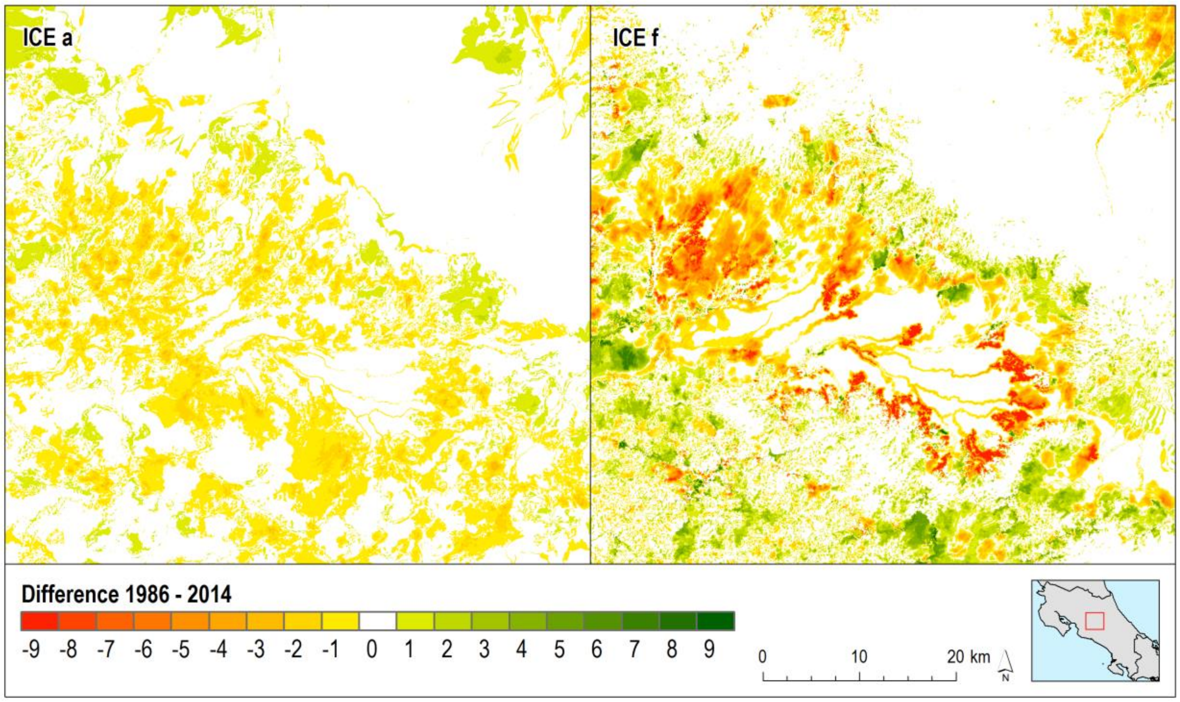

Source: Own elaboration from the REDD+ national program (Fernández-Landa et al. 2016)

**Fig. 3** Land cover changes in the Central Valley of Costa Rica (1986-2014)



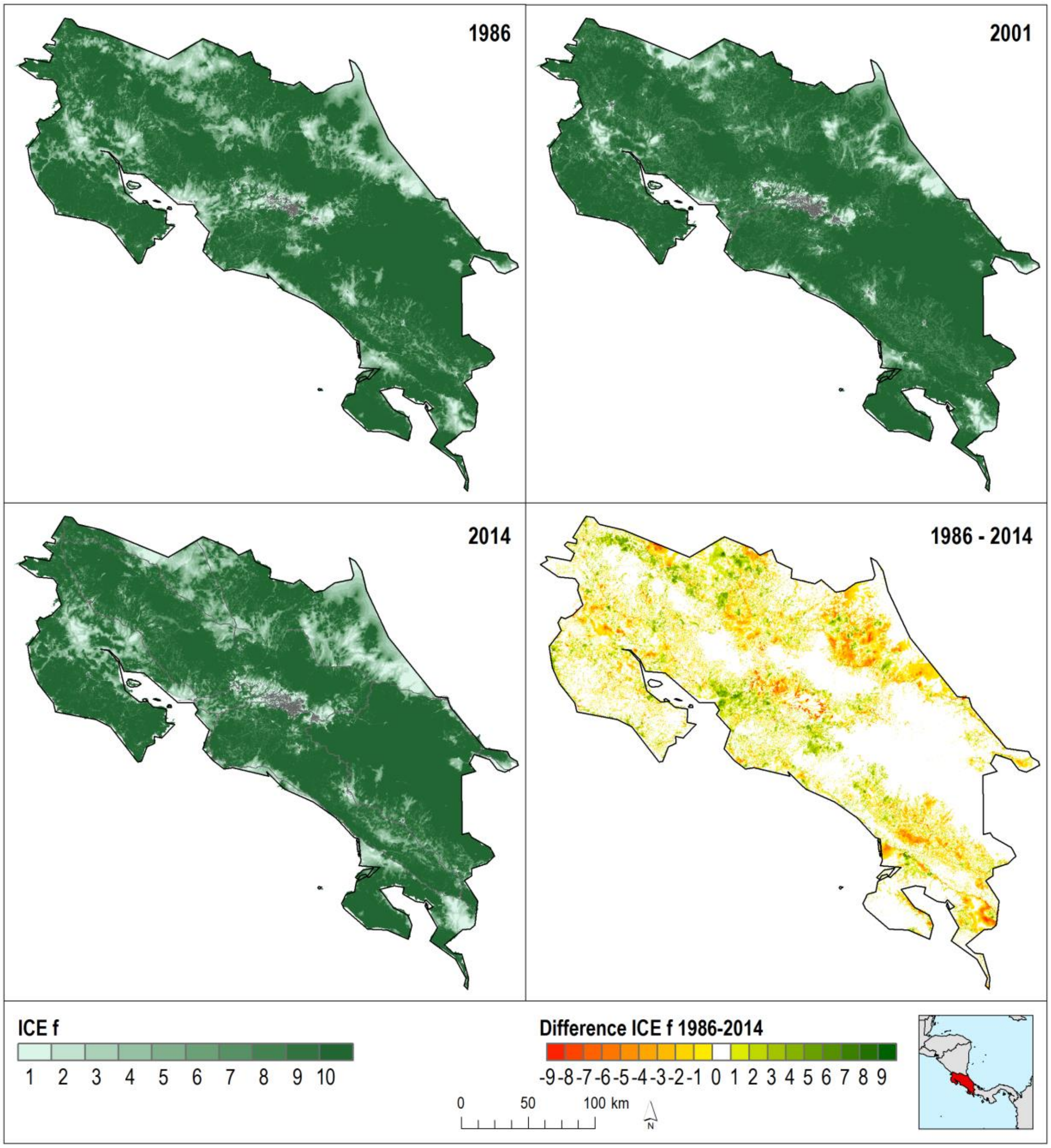

Source: Our own

**Fig. 4** Differences in the Ecological Connectivity Index (1986-2014) in forestland ($ECI_f$) and in the whole land-matrix ($ECI_a$) of the Central Valley



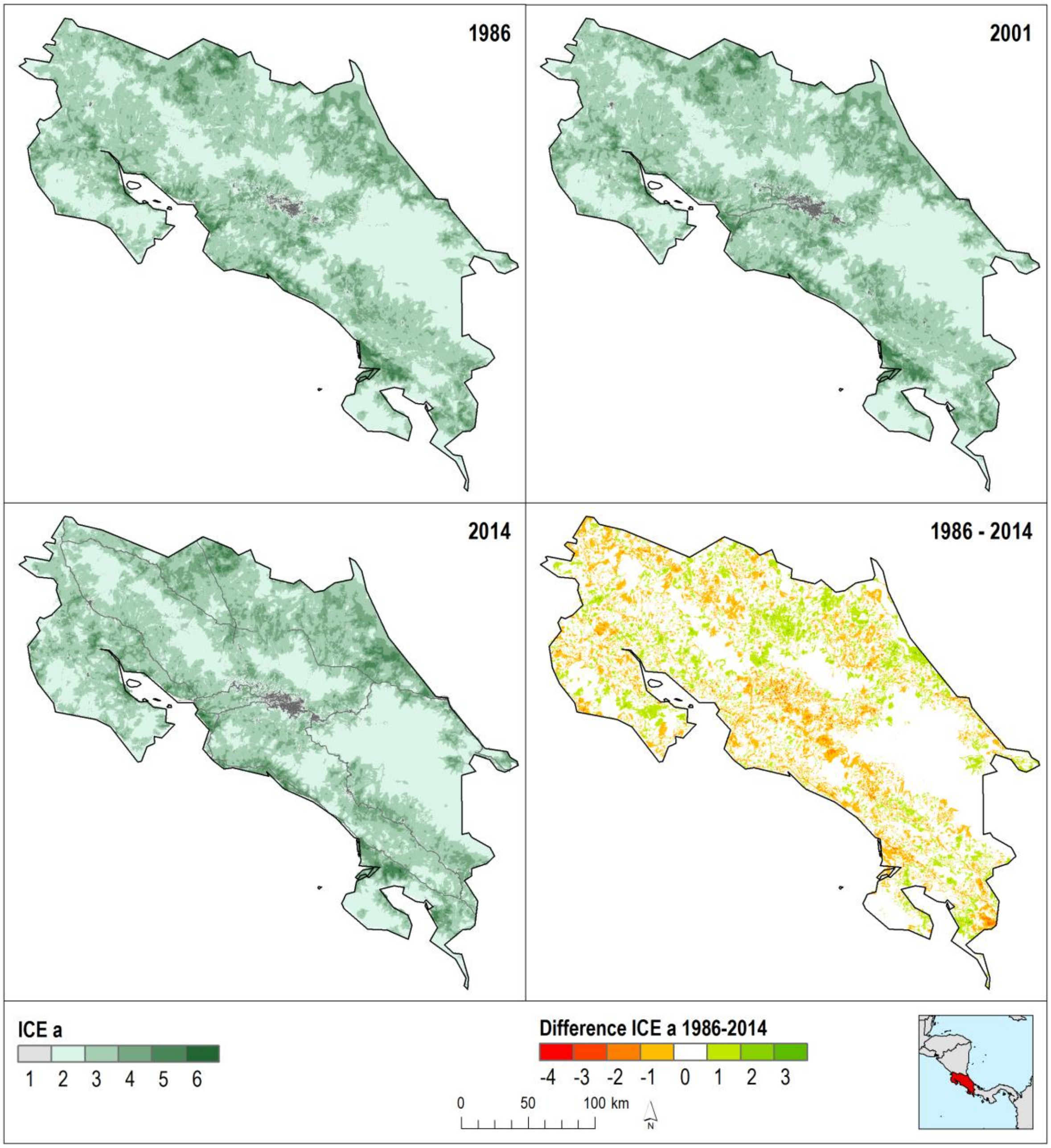

Source: Our own

**Fig. 5** Map of the forestland basic Ecological Connectivity Index $ECI_f$ (1986-2011-2014)



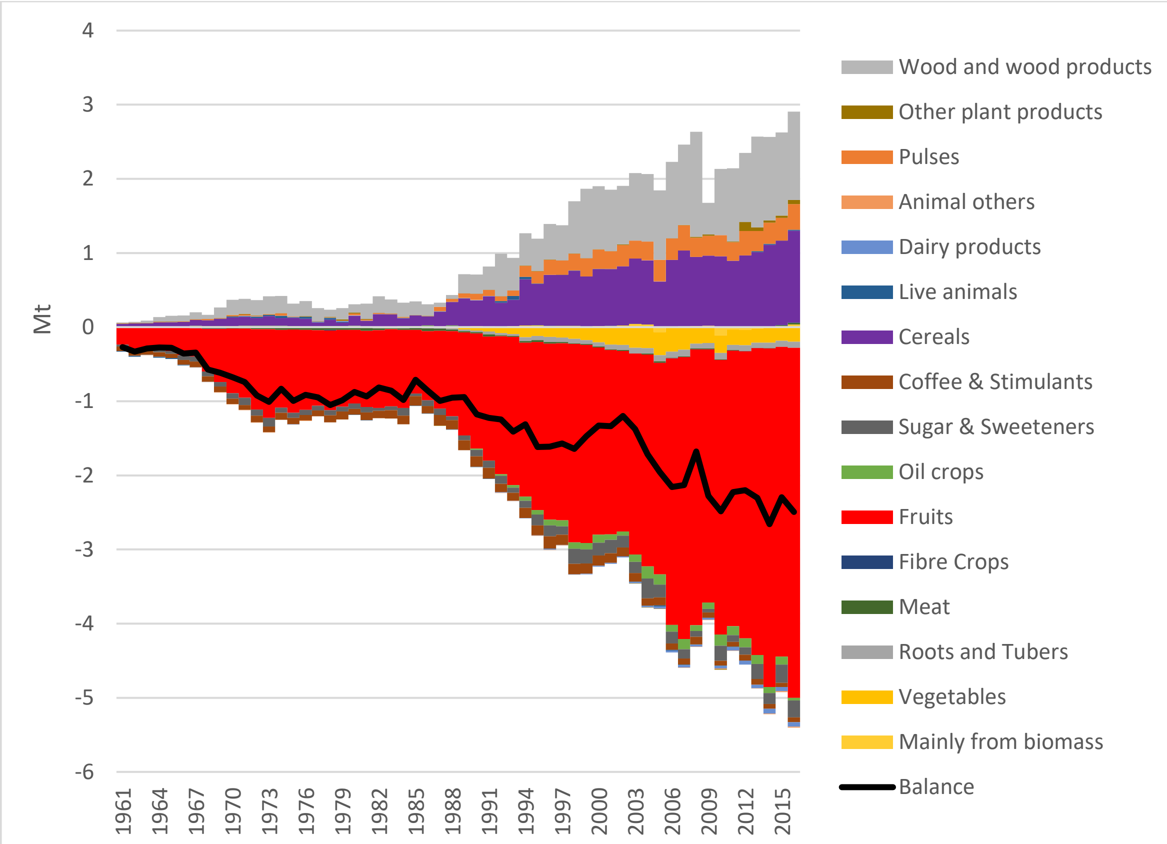

Source: Our own

**Fig. 6** Map of the absolute Ecological Connectivity Index ($ECI_a$) in the whole land-matrix (1986-2011-2014)



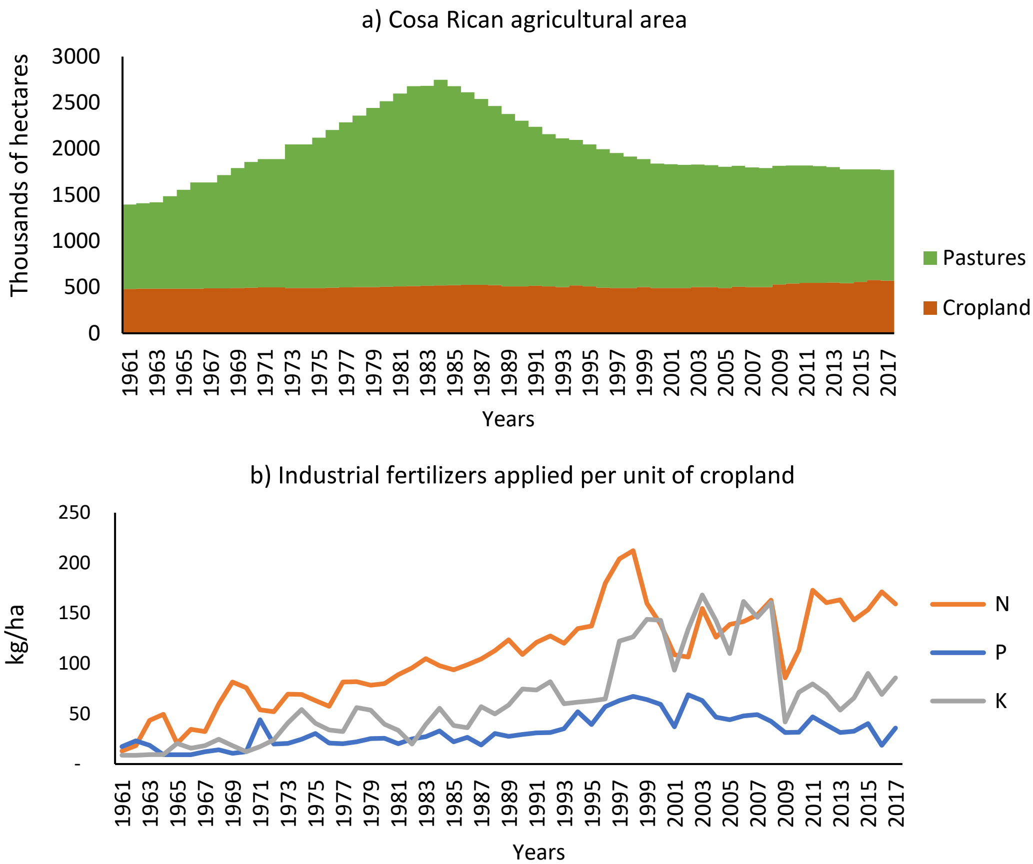

Source: Our own

**Fig. 7** Physical Food Trade Balance of Costa Rica (1961-2016)




Source: Our own elaboration from Faostat. Negative values are exports, and positive imports.

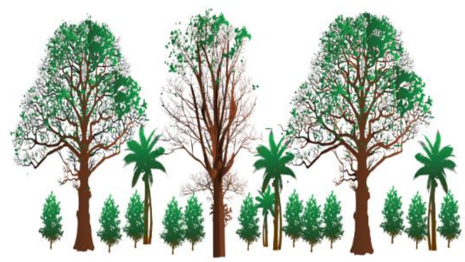
**Fig. 8** Agricultural area (a) and average doses of industrial fertilizers per hectare (b) in Costa Rica (1961-2016)



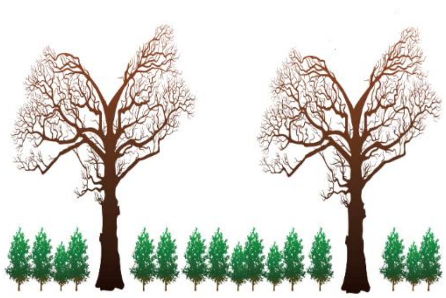

Source: Our own elaboration from Faostat.

**Fig. 9** Scheme of different coffee-farming systems in Costa Rica (from rustic agroforestry and coffee polyculture to shade grown and coffee monoculture)

Rustic Coffee Agroforestry



Coffee Polyculture



Shade-grown Coffee Plantation

Sun-grown Coffee Monoculture

Source: Own elaboration from Fournier (1980)

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