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ORIGINAL ARTICLE

Dynamics of tropical forest regeneration in the Mexican Mesoamerican Biological Corridor from 2000 to 2020: does forest regeneration maintain continuous forest cover?

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Abstract

Forest dynamics in the Mexican Mesoamerican Biological Corridor (MxMBC) have been part of a land sharing system, helping maintain forest cover following semi-subsistence land-use through regeneration. Recently, mechanized cash-crop cultivation is occurring, translated in larger, permanent tracts of agriculture in place of core forest. This emerging land-use marks a potential shift in regeneration patterns, with implications for the maintenance of forest cover. We characterize MxMBC forest regeneration patterns from 2000 to 2020 to assess their relationship with the maintenance and expansion of forest cover. Classification of multi-temporal remotely sensed Landsat data reveals a decrease of 2.2% (296 km^2) of forest area from 2000 to 2020, with regrowth making back 0.93% of forest (121 km^2) by 2020. A spatial model identifies that 75.1% of forest regeneration in the study site occurs in four patterns ranging from permanent (89.2 km^2, 41.7%) to ephemeral (71.5 km^2, 33.4%). Analyzing the relation between landscape configuration and forest regeneration shows that regrowth occurs in small, widely dispersed forest patches. Spatial patterns of ephemeral regeneration mark two distinct land sharing contexts — ephemeral regeneration buffering core forest loss alongside semi-subsistence agriculture and agroforestry, and ephemeral regeneration masking core forest loss alongside cash crop agriculture. These cases suggest that maintaining forest cover through regeneration is impacted by land-use context, as the regeneration to core forest ratio decreases when permanent cash crop cultivation emerges.

Keywords Mexico · Tropical forest regeneration · Land sharing · Conservation · Fragmentation

Introduction

Dynamic and simultaneous processes of deforestation and regrowth are impacting tropical regions globally, with nearly 1/3 of cleared old growth regenerating through secondary forest succession (Arroyo-Rodríguez et al. 2017). Contributing to a global increase in secondary forest cover from 2000 to 2012 (Arroyo-Rodríguez et al. 2017), reforestation in Latin America and the Caribbean over the same time period accounts for a large proportion of pantropical reforestation (Nanni et al. 2019), with a reported 360,000 km^2 increase in woody vegetation (Schwartz et al. 2020) making back about 66% of deforested regions (Aide et al. 2013). Regenerating forests are part of heterogeneous landscapes, as diverse disturbances transform old-growth forest into mosaics of agriculture, settlement, and regenerating forest patches of multiple successional stages. In Latin America, regenerating forests are an important component of human occupied forested landscapes, integrated into both agriculture (i.e., swidden cultivation) and conservation planning to maintain and enhance biodiversity, provide climate services, and sustain livelihoods (Uriarte et al. 2004; Quesada et al. 2009; Aide et al. 2013; Arroyo-Rodríguez et al. 2017). At the same time, forest regeneration ranges from ephemeral to permanent (Chazdon et al. 2016; Nanni et al. 2019; Schwartz et al. 2020), and from discontinuous forest patches to continuous tracts of land preserved for afforestation. Thus, the spatio-temporal patterns of forest regeneration have implications for broader forest landscape configurations and the

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potential of these landscapes to maintain forest cover and ecosystem processes.

The land sparing and land sharing frameworks have been highlighted as opportunities to balance forest conservation and land-use (Phalan et al. 2011; Grau et al. 2013). The frameworks propose two strategies to address the simultaneous challenges of conservation and commodity production through the process of forest regeneration (Loconto et al. 2020). First, land sparing aims to segregate areas of land-use and forest preservation, suggesting that agricultural intensification on smaller land areas can set aside less productive land to regrow (Waggoner 1994; Phalan et al. 2011). Second, land sharing integrates areas of land-use and conservation, with the idea that smaller preserved regeneration areas alongside less intensive production can maintain some biodiversity within an agricultural landscape matrix (Perfecto and Vandermeer 2010). The conservation and environmental benefits of both land sparing and land sharing have been debated (Ewers et al. 2009; Rudel et al. 2009; Kremen 2015). However, the relationship of forest regeneration and landscape configurations may be more complex than the dichotomy of land sparing or land sharing alone, challenging the noted socio-ecological benefits of either (Kremen 2015). For example, numerous afforested regions in Latin America have high settlement densities with diverse land-uses alongside larger contiguous tracks of agricultural production (both land sparing and land sharing) (Aide et al. 2013; Hecht 2014).

Forest dynamics research across the neotropics shows how forest regeneration is a dynamic spatio-temporal process, operating at multiple scales, and directly influenced by the local socio-ecological conditions of particular environments, disturbances, and land-uses (Chokkalingam and de Jong 2001; Chazdon et al. 2016; Schwartz et al. 2020). Monitoring these dynamics, predominantly through remote sensing, has been critical for understanding socio-ecological drivers associated with forest cover change and for projecting changes into the future (Houet et al. 2010). However, there is a need for better detection of subtle land cover changes, such as regenerating forest patches in heterogeneous landscapes of agricultural lands inside mature forest, managed through land-sparing and land sharing strategies (Houet et al. 2010). Accurately characterizing subtle changes, such as forest regeneration in former agricultural lands, ultimately enhances monitoring, projection, and decision making associated with landscape change by better integrating past and current landscape configurations and their feedbacks with management goals such as conservation (Teixeira et al. 2009; Houet et al. 2010). Despite this, current understanding of Latin American tropical forest regeneration is dominated by plot level vegetation composition and structure (i.e., Hernández-Stefanoni et al. 2011; Dupuy et al. 2012), and regionally is drawn predominantly from continental-scale reviews of deforestation and regeneration (i.e., Aide et al. 2013; Arroyo-Rodríguez et al. 2017; Chazdon et al. 2016; Schwartz et al. 2020). Given the specific socio-ecological contexts that influence spatial patterns of tropical forest cover, subtle changes such as forest regeneration are at risk of being generalized in continental scale findings, or taken out of context when regional conclusions are applied to multiple local forest environments. Furthermore, many regional analyses of forest regeneration are restricted to a snapshot of forest cover between two time periods, or through linear modeling of time-series data, and simple characterizations of forest cover change as either deforestation, reforestation, or no change (Southworth et al. 2004; Schwartz et al. 2020).

Broad spatio-temporal characterizations mask dynamics of smaller scale forest conversions and resulting configurations, as forest cover change is recognized as a non-equilibrium, spatial process (Chokkalingam and de Jong 2001; Schwartz et al. 2020). For example, in the Mesoamerican Biological Corridor (MBC), a region-wide conservation initiative spanning Central America and Southern Mexico, both land sharing and land-sparing systems exist with aims to satisfy the main goal of this corridor — to simultaneously conserve biodiversity and promote sustainable development often through reforestation initiatives (Miller et al. 2001; Harvey et al. 2008). Countries in the MBC have been identified as “reforestation hotspots,” where forest regeneration occurs in high populous regions alongside multiple land-use types and intensities, stages of permanence, and risk levels of transforming to alternate land covers (Nanni et al. 2019; Schwartz et al. 2020). Within snapshots of net deforestation, reforestation, and assessed “no change” are smaller spatio-temporal scale forest conversions ranging from permanent to ephemeral, across consecutive and non-consecutive time intervals. Combining these smaller scale conversions and forest configurations from multiple intervals highlights the role of forest regeneration as a subtle land cover change in a broader landscape matrix. For example, examining forest conversions and configurations across multiple intervals in the MBC can show the role that regenerating forest patches play in achieving the balance of conservation and land-use, where regeneration can either contribute to forest expansion as a set aside from certain land-use initiatives, maintain mature and core forest in the landscape matrix as part of continuous deforestation-regrowth cycles in a single area, or increase forest fragmentation if cycles of deforestation and regrowth are expanding into areas of mature and core forest.

At the northern margin of the conservation corridor, the Mexican section of the MBC has been designated a hotspot for biodiversity conservation and deforestation (Klepeis and Turner 2001; Schneider et al. 2016). Here, secondary forests are part of a land sharing system that combines shifting cultivation, agroforestry, regenerating abandoned pastures, replanted plantations, and forest regeneration from windfall

(Ellis et al. 2017a, b). However, the emergence of intensified agriculture through mechanized cash-crop cultivation in some regions of the Mexican portion of the MBC, mirroring trends seen in other MBC regions (Fagan et al. 2013), could signal a change in the role of forest regeneration for land-use and a subsequent change in forest configuration characteristic of land sparing. Combining forest dynamics (forest loss, forest gain, and no change) across multiple intervals highlights regeneration patterns ranging from permanent to ephemeral and consecutive to non-consecutive in the MBC of Mexico, and further can be compared to forest landscape configurations through time to clarify the influence of evolving land-uses on spatial patterns of forest regrowth.

In this article, we characterize spatial and temporal patterns of forest regeneration in a portion of the Mexican MBC from 2000 to 2020, a period encompassing major environmental disturbances (i.e., Category 5 hurricane Dean in 2007), and local level and diverse changes to land-use practices (i.e., rise of mechanized cash crop cultivation). Using segmentation analysis of Landsat Satellite imagery and a three-step cartographic model, we quantify the major spatio-temporal patterns of forest regeneration across a portion of the Mexican MBC and statistically determine the relationship between forest regeneration and landscape configuration. Given emerging regional land-use practices, we hypothesize that forest regeneration is associated with a decrease in fragmentation and increase in core forest, characteristic of land sparing landscapes instead of land sharing, which are expected in semi-subsistence regions across the MBC.

Study site, data, and methods

Study site

This study spans a 17,199-km^2 area of the MBC in Mexico situated between the protected areas of Sian Ka'an, to the northeast of the study site on the Gulf Coast of the Yucatán Peninsula, and the Calakmul Biosphere Reserve along the western margin (herein called the MxMBC) (Fig. 1). The MxMBC is characterized by seasonally dry tropical forest of varying types and structures (Schmook et al. 2011). Deciduous and semi-deciduous forests predominate inland, with mid-statured forests on well-drained terrain, and low-statured forests on seasonally inundated low-lying areas (Ellis and Porter-Bolland 2008; Cuba et al. 2013). Deciduous forests predominate the northwest and extend to the southeast along a precipitation gradient (Vester et al. 2007). Wetlands and mangroves predominate the east, particularly in lowland coastal regions (Ellis and Beck 2004; Vester et al. 2007). Periodic environmental disturbances such as drought (Mendoza et al. 2007; Mendez and Magana 2010; Schneider et al. 2016) and hurricanes (Boose et al. 2003; Rogan et al. 2011; Schneider et al. 2016) impact MxMBC forests.

Land tenure in the MxMBC is characterized by *ejidos*, or communally managed land areas, within which decisions on land-use are made by the community at large (Roy Chowdhury 2010; Turner et al. 2016). The study site comprises 156 *ejidos* across 5 different municipalities, with an average *ejido* size of 81.8 km^2 (Fig. 1). *Ejidos* in the MxMBC were established in two waves, initially in the 1930s to 1940s, and again in the 1960s, to convert forest into more economically valuable land-uses (Perramond 2008; Turner et al 2016). While some land-uses are common across all municipalities, such as logging of hardwoods (Klepeis et al. 2004), semi-subsistence swidden agriculture focused predominantly on maize (*milpa)* (Klepeis et al. 2004; Schmook 2010), and pasture conversion for livestock (Schneider and Fernando 2010; Busch and Vance 2011), variation in land-use among municipalities exists. For example, conservation initiatives and sustainable development policies have promoted semi-subsistence swidden agriculture within and outside conserved forest of the Calakmul Biosphere Reserve in *ejidos* of municipality Calakmul and southern *ejidos* of municipality Hopelchén. Community-managed semi-subsistence and commercial forestry practices predominate the *ejidos* of municipality Felipe Carrillo Puerto and northeastern *ejidos* of Othón P. Blanco (Ellis and Porter-Bolland 2008). More recently, agricultural expansion into cash crop cultivation of sugarcane, corn, pineapples, and beans has been prevalent, particularly in the municipalities of Othón P. Blanco, José Maria Morelos, and Hopelchén, alongside traditional semi-subsistence agriculture (Roy Chowdhury 2006; Ellis and Porter-Bolland 2008; Miteva et al. 2019; Ellis et al. 2020) (SIFig. 1). Taken together, periodic environmental disturbance, shifting agriculture that incorporates forest regeneration, and more recent, permanent cropland result in a patchwork of forest configurations across the MxMBC.

Data

Eight atmospherically and geometrically corrected cloudless image composites corresponding to individual years were selected from a Landsat satellite image series spanning 2000–2020, two image scenes (Path 19 Row 47, Path 20 Row 47), and two generations of Landsat sensors (Landsat 7 ETM+, Landsat 8 OLI) (SITable 1; Fig. 2). We limited image collection to the dry season (January 1 to May 1) to reduce cloud cover and to ensure spectral separability among deciduous forest and agriculture, as planting and harvesting occur in the wet season. Only images containing < 10% of missing pixel values from cloud cover masking before compositing were selected for analysis, resulting in Landsat composites for eight individual image years between 2000 and 2020 (SITable 1; Fig. 2). A scan line fill algorithm was

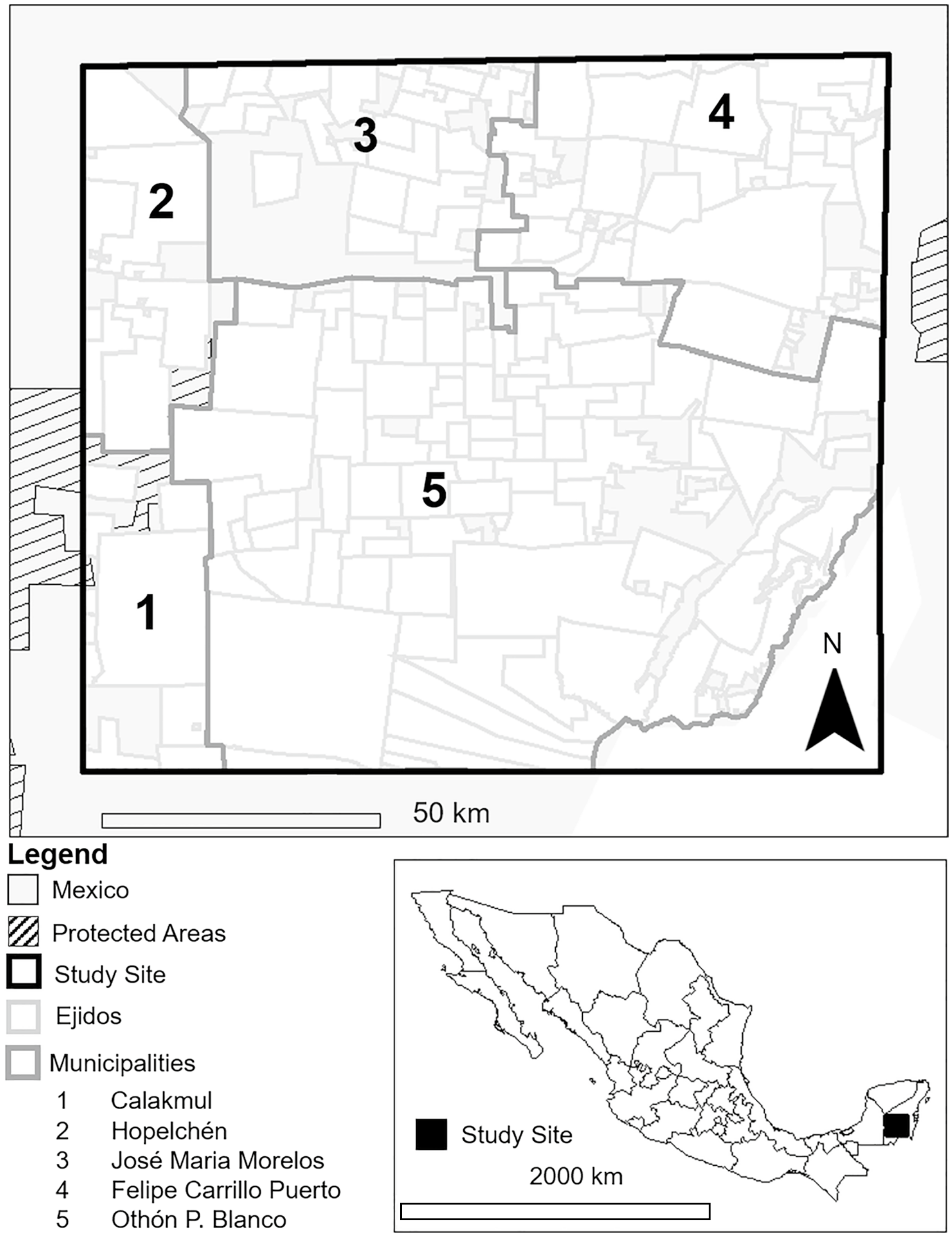

Fig. 1 Map of the study site (MxMBC), spanning a 17,199 km^2 area of the MBC in Mexico between the Calakmul and Sian Ka'an Biosphere Reserves in the Southeastern portion of the Yucatan Peninsula, Mexico. The MxMBC comprises 156 *ejidos* across (light grey outlines) 5 municipalities (dark grey outlines, numbered)

used to fill data gaps in the Landsat 7 ETM + images (2007, 2010) from the failed scan line corrector. Annual image composites from 2000 to 2020 were created by extracting the median reflectance value for each pixel from all available dry season images for each respective year.

Reference data assisted training site selection (600 training sites total, 50 each for 12 distinct vegetation and land use classes), accuracy assessment, and image sampling for statistical analysis (SITable 1). Land cover information from in situ forest plots (McGroddy et al. 2013; Vandecar et al. 2011; Zager, 2014) was used for training site selection and accuracy assessment. Two published landcover maps from 2000 and 2010 identified training sites for classification of the image composites (Schmook et al. 2011; Zager 2014). A polygon shapefile of 156 *ejidos* across the study site contained information about each *ejido*'s respective municipality (five in total), provided by the Mexican Government's National Agricultural Registry (Registro Agrario Nacional, 2017). All spatial data were represented using the Universal Trans Mercator (UTM) Zone 16 North Coordinate System and the World Geodetic Survey 1984 Datum.

Forest regeneration mapping

To create binary forest-non forest cover maps (herein referred to as forest-non forest maps) for each of the eight

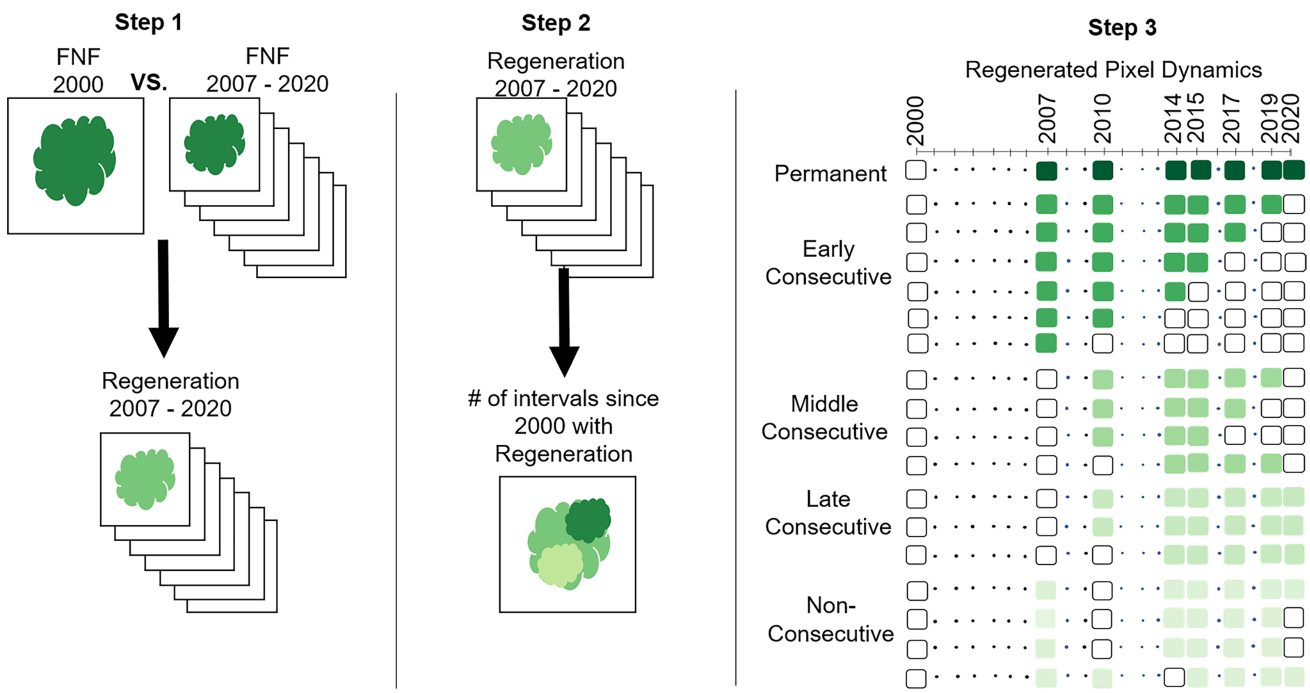

Fig. 2 A 3-step cartographic model used to classify 18 different patterns of forest regeneration dynamics from 8 individual forest non-forest cover maps. Empty squares shown in the regenerated pixel dynamics diagram of step 3 represent non-forest

image composites, we classified land covers using reflectance values from 5-bands of the image composites (i.e., blue, green, red, near infrared, and short wave infrared 1 bands (SIFig. 2)), signature file training through supervised segmentation, and minimum distance supervised classification algorithm. Segmentation uses an object-based approach to signature file development by defining homogenous pixels into spectrally similar segments, facilitating the creation of spectrally distinct land cover signatures for supervised classification (Schneider et al. 2018) (SIFig. 1). At least 25 individual 50 m threshold polygons from image segmentation were manually selected to define twelve distinct classification signatures for land-uses and vegetation types across the study site, chosen due to a combination of the reference data and image interpretation based on polygon geometry, texture, and pixel values (SITable 2). The resulting twelve land cover signatures informed minimum distance supervised classification. Following, the twelve classified land-use and vegetation types were fit to five broad land cover classes (water, urban, marsh, agriculture and pasture, and forest), corresponding to spectrally distinct training sites (spectral separability metric, average transformed divergence value > 1800), and were further generalized to either a forest or non-forest class (SIFig. 1; SITable 2; SIFig. 2).

Classification accuracy was assessed by comparing forest and non-forest classes of the 8 forest-non forest maps to cover information from the reference data, the original composite images, and imagery of higher spatial resolution, when available. A total of 100 sample points were generated through equalized random sampling to assess the overall, user's, and producer's accuracy of the forest-non forest classes in a contingency table. Furthermore, due to the inherently small proportion of non-forest to forest area across the study site (SITable 3), we assured discrete forest and non-forest classes using an iterative statistical thresholding process on both classes (Wang and Civco 1992). This process ensured a high probability that regenerated forest classes were a product of "pure" forest and non-forest pixel dynamics through time as opposed to the presence and misclassification of "mixed" pixels. We manually identified a threshold along a histogram of chi-squared Euclidian spectral distance values for each pixel, representing the distance between an individual pixel's reflectance values and the mean spectral reflectance for the pixel's respective class and image year (SIFig. 3). Resulting spectral distance values in histogram tails are "far" from the reflectance values of the class signature mean (Wang and Civco 1993) (SIFig. 3). Therefore, pixels with distance values in the histogram tails, beyond the threshold, were assumed to have a higher probability of being mixed forest and non-forest covers and eliminated from further analysis (SIFig. 3, SIFig. 4). For every individual user-defined threshold, we erred on the side of eliminating more pixels through the thresholding process than necessary from further analysis over maintaining the potentially "mixed" or erroneous pixels (SIFig. 3).

Annual deforestation rates for eight-time intervals was calculated from the forest-non forest maps using the annual deforestation rate equation from Puyravaud (2003) as follows:

$$r = \left(\frac{1}{t2 - t1}\right) x \ln\left(\frac{A2}{A1}\right) \quad (1)$$

where the percentage of annual forest cover change (r) is dependent on the amount of forest cover (A) at both time t1 and t2. Additionally, the 2000 and 2020 land cover maps were generalized to binary agriculture-non agriculture cover to analyze changes in agricultural patch size.

We input the 8 binary forest cover maps into a 3-step cartographic model (i.e., spatial analysis based on spatial as opposed to mathematical relationships) (Fig. 2) to derive one map of spatially explicit regenerating forest patterns (2000–2020), classified by consecutiveness, or how many intervals regeneration occurred, and the timing of when this regeneration occurred within the study period. We classified pixels as regenerated if they transition from non-forest to forest cover at any time since 2000 and remain forest cover after at least 5 years has passed between study intervals. The 3-step model is as follows: (1) We created seven individual forest regeneration maps through homogenous univariate decision-tree classification of the 2000 forest-non forest map and remaining seven forest-non forest maps, respectively. This process classified pixels as regenerated if a pixel, originally non-forest in 2000, transitioned to a forest pixel in each respective year afterwards; (2) We combined the resulting seven individual forest regeneration maps using map algebra to create a single map of regeneration, where pixels are classified by how many individual intervals regeneration occurs between 2000 and 2020; and (3) We used a series of conditional statements to organize each regeneration class into 18 possible forest regeneration patterns, first by level of consecutiveness (permanent, ephemeral consecutive, and ephemeral non-consecutive) and second by the timing of when regeneration occurred between 2000 and 2020 (Fig. 2). The first level of consecutiveness is permanent, classified if a pixel, originally non-forest in 2000, transitioned to a forest pixel for all remaining intervals between 2007 and 2020. Second, the stages of early, middle, and late ephemeral consecutive regeneration were defined when a pixel, originally classified as non-forest in 2000, transitions to and remains forest for multiple consecutive time intervals, clustered at the beginning, middle, or end of the time period, respectively. Third, ephemeral non-consecutive regeneration was classified when a pixel, originally non-forest in 2000, transitions to forest in multiple, non-consecutive time intervals between 2007 and 2020 (Fig. 2).

Measuring forest landscape configuration

We derived measurements of landscape configuration from forest-non forest maps using the Morphological Spatial Pattern Analysis (MSPA) tool in the GuidosToolbox v 2.7 and from the agriculture-non agriculture cover maps using the Fragstats v. 4.2 programs. We defined landscape configuration in terms of fragmentation variables (i.e., core, islets, perforation, edge) and agricultural land-use footprint (i.e., mean area of agriculture cover patches), calculated at the *ejido* level for 156 *ejidos* within 5 municipalities of the MxMBC.

To characterize core, islets, perforation, and edge for 2000 and 2020, we used a 30-m edge width, equivalent to the spatial resolution of input maps, and a Queen's neighborhood connectivity rule as analysis parameters. Since our focal class of interest was forest, we used four main variables to understand landscape configuration across the study site: *Core,* defined as forest pixels surrounded by forest on all sides; *Perforation*, defined as pixels that form a transition between forest and non-forest areas within the core; *Islets*, defined as forest patches outside of core and that are too small to contain core forest; and *Edge*, or pixels that form the transition between forest and non-forest areas. To measure land-use footprint, binary agriculture cover maps from 2000 and 2020 were input into the Fragstats program to calculate the mean agriculture cover patch size for both years.

Fragmentation variables were measured from 0 to 100, calculated as a percent of the amount of forest present in each individual *ejido* ($n = 156$). The following indices were estimated for 2000 and 2020: core, perforation, islets, and edge. We estimated a fragmentation index by dividing the percentage of forest classified as edge by the percentage of forest classified as core. The fragmentation index provides a value from 0 to 1, where 1 describes the highest level of fragmentation and 0 describes no fragmentation (Zager 2014).

Statistical analysis

We calculated area of total regeneration, area of individual regeneration patterns, fragmentation variables (i.e., core, islets, perforation, and fragmentation indices), and land-use footprint (mean patch size of agriculture cover) within 156 *ejido* polygons (Fig. 1). Total area of regeneration and area of individual regeneration patterns were standardized as a percentage of the total area of each *ejido*, while fragmentation variables were calculated as a percentage of forest cover area within each respective *ejido*. Data are characterized as non-parametric as they did not meet the assumption of normal distribution at the scales of analysis. To examine regional differences, we used a Kruskall Wallis test to examine if statistically significant differences in total regeneration, individual regeneration patterns, changes to fragmentation variables, and changes to mean agriculture patch size exist between *ejidos* within five municipalities in the study site (Fig. 1). Furthermore, a Wilcoxon signed-rank test identified between which municipalities statistically significant differences in *ejido* level forest regeneration, changes to fragmentation variables, and changes to mean agriculture patch size occurred. We estimated the association, and potential change in association through time, between total regeneration, forest regeneration patterns, fragmentation variables, and mean agriculture patch size at the *ejido* level in both 2000 and 2020 using Spearman's Rank-Order correlations.

Results

Accuracy of the forest-non forest maps ranged from 84 to 91% (SITable 5). The user's accuracy, or the probability that the classes accurately represented land cover on the ground, range from 86 to 98% for forest and 76 to 90% for non-forest (SITable 5). The producer's accuracy, or the probability that ground covers were correctly classified, ranged from 76 to 89% for forest and 86 to 97% for non-forest (SITable 5).

From area classified as forest in 2000, the study site experienced simultaneous decrease of 2.2% of forest (total loss of 296 km^2) and regrowth of 0.93% of forest (121 km^2) by 2020 (Table 1; SITable 4). Furthermore, the net annual rate of forest cover loss, proportional to the total study area (– 0.092% annually, – 0.003 km^2a^{-1}) is larger than the net annual rate of proportional forest cover gain (+ 0.045% annually, + 0.002 km^2a^{-1}) (SITable 4). Annual rates of forest loss for 2010–2014 and 2017–2019 are higher than gain, with deforestation rates of 0.825% and – 2.86%, respectively (Fig. 3; SITable 4; SIFig. 5). The inverse occurs from 2007 to 2010, 2014 to 2015, and 2015 to 2017, with annual rates of proportional forest cover gain larger than forest cover loss and annual afforestation rates of + 1.00%, + 3.93%, and + 0.904%, respectively (Fig. 3; SITable 4). Nearly equivalent annual rates of proportional forest cover gain to loss are seen from 2000 to 2007 and 2019 to 2020, with deforestation rates of – 0.093% and – 0.583, respectively (Fig. 3, SITable 4).

Table 1 Total classified forest area (km^2) of each classified image composite, and the corresponding area of that total forest for each year that has been classified as regenerated since 2000 (km^2)

Forest area (km^2) in 2000: 13,251
Non forest area (km^2) in 2000: 1394

Year	Total forest (km^2)	Percent of study site classified as forest (%)	Regenerated forest since 2000 (km^2)	Proportion of total forest area classified as regenerated (%)
2007	11,917	89.9	174	1.46
2010	13,900	92.6	183	1.32
2014	10,561	89.5	193	1.83
2015	12,437	93.1	202	1.63
2017	12,739	94.7	200	1.57
2019	12,376	89.3	191	1.54
2020	12,956	88.8	121	0.93

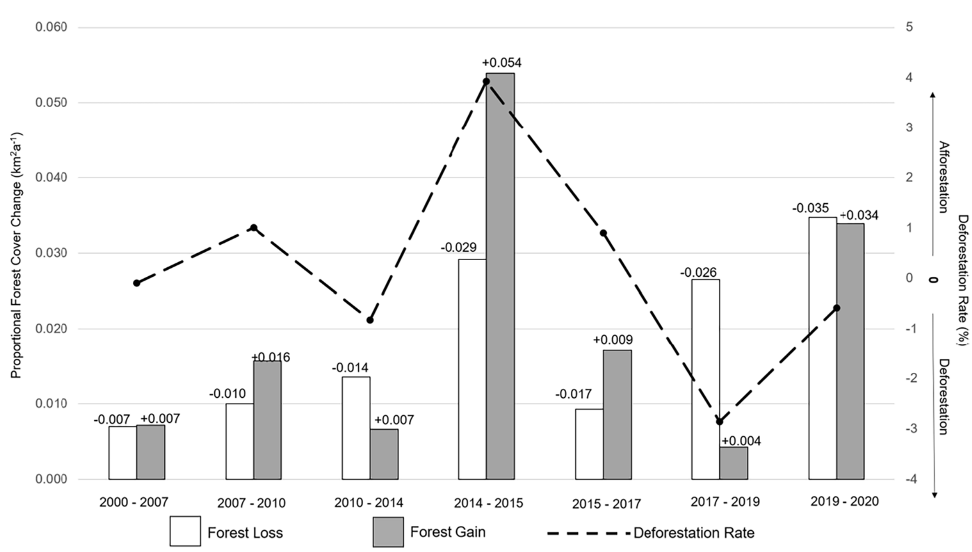

Fig. 3 The annual rate of proportional forest cover loss and gain (km^2a^{-1}) is plotted across seven time intervals between 2000 and 2020 along the primary axis. The annual deforestation rate (%) for each of the seven time intervals is plotted along the secondary axis, where positive values indicate afforestation and negative values indicate deforestation

Spatio-temporal patterns of forest regeneration in the Mexican Mesoamerican Biological Corridor (2000–2019)

Of all pixels that transition from non-forest in 2000 to forest in subsequent intervals, 214 km^2 fit within our definition of regenerated forest pixels across 18 regeneration patterns. Forest regeneration in the MxMBC is comprised predominantly of permanent regeneration (89.2 km^2, 41.7% of regenerated forest area), and ephemeral consecutive regeneration over 6 intervals between 2007 and 2019 (CEA, 47.1 km^2, 22.0% of regenerated forest area), over 6 intervals between 2010 and 2020 (CLA, 13.7 km^2, 6.41% of regenerated forest area), and over 5 intervals between 2010 and 2019 (CMA10.7 km^2, 4.99% of regenerated forest area) (SIFig. 6). Together, both permanent and ephemeral consecutive CEA, CLA, and CMA patterns of forest regeneration account for 75.1% of total regeneration. Ephemeral patterns of consecutive and non-consecutive regeneration are found predominantly scattered around the edge of and within agricultural areas of semi-subsistence swidden agriculture, agroforestry, and cash crop agriculture (Fig. 4). Furthermore, regeneration of all patterns emerges as small, non-contiguous forest patches (Fig. 4).

Relationship of regeneration to forest configuration

Kruskall Wallis and Wilcoxon tests identified statistically significant differences in the percent of *ejido* area classified as total regeneration (permanent, and ephemeral CEA, CLA, and CMA regeneration, combined) ($Pr(>f) = 2.51 \times 10^{-8}$), and percent area classified as permanent ($Pr(>f) = 5.20 \times 10^{-5}$), CEA ($Pr(>f) = 1.158 \times 10^{-7}$), CMA ($Pr(>f) = 0.003$), and CLA ($Pr(>f) = 0.020$) (SI Table 6, Fig. 5). Percent area of total regeneration, permanent regeneration, and CEA regeneration is significantly larger in *ejidos* of Othón P. Blanco than in *ejidos* of all other municipalities (Fig. 5, SITable 6). Percent area of both CMA and CLA regeneration is significantly larger in *eijdos of* Othón P. Blanco than in ejidos of Calakmul, José Maria Morelos, and Felipe Carrillo Puerto, but not statistically different than those in Hopelchén (Fig. 5, SITable 6). Statistically significant differences in fragmentation index change (2000–2020) occurred ($Pr\ (>f) = 5.897 \times 10^{-5}$), with a mean increase in fragmentation in Othón P. Blanco (mean = +0.128, SD = 0.096) larger than in ejidos of José Maria Morelos (mean = +0.066, SD = 0.108), Felipe Carrillo Puerto (mean = +0.064, SD = 0.081), and Calakmul (mean = +0.019, SD = 0.044). Similarly, statistically significant differences in core index change (2000–2020) occurred ($Pr(>f) = 0.0002$), with a mean decrease in core forest in Othón P. Blanco (mean = −9.06, SD = 6.21) larger than in ejidos of José Maria Morelos (mean = −5.02, SD = 7.73), Felipe Carrillo Puerto (mean = −4.96, SD = 5.07), and Calakmul (mean = −1.67, SD = 4.06) (Fig. 5, SITable 6). Kruskal Wallis tests found no statistically significant difference in changes to mean agricultural patch size.

Ejidos of municipality Othón P. Blanco saw the highest mean percent of regeneration in all patterns alongside the largest average increases in fragmentation index (+0.128) and largest average decreases in core index (−9.06) of all municipalities (SITable 6). *Ejidos* of Hopelchén did not record significant differences in forest regeneration or forest configuration indices than *ejidos* of other municipalities, although *ejidos* of Hopelchén had the second largest mean percent of regeneration in all patterns, alongside the second largest increase in mean fragmentation index value (mean = +0.104, SD = 0.126) and second largest decrease of mean core forest index (mean = −7.72, SD = 8.82) (Fig. 5, SITable 6). The range of mean agriculture patch size changes was largest in *ejidos* of Hopelchén and Othón P. Blanco, with the largest increase in mean agriculture patch size recorded in Othón P. Blanco (mean = +58.6, SD = 343), indicating diverse agricultural land-use and plot size changes in *ejidos* of both municipalities alongside an average increase in mean agriculture patch size in *ejidos* of Othón P. Blanco (SITable 6).

Results from Spearman's Rank-Order Correlation Analysis show forest regeneration occurs in fragmented forest landscapes. Total proportional area of regeneration is negatively associated with the core forest index, and positively correlated with the forest fragmentation index (Table 2). This pattern holds in both 2000 and 2020, although the relationship in 2000 is stronger (P-value < 0.05) (Table 2). All regeneration patterns show positive and statistically significant correlation with the islet and perforated forest index in both 2000 and 2020 (Table 2). Furthermore, all regeneration measures are positively associated with mean agriculture patch size indicating increased area of regeneration with increasing agricultural patch size, with the strongest relationship recorded with ephemeral CEA regeneration (Table 2).

Discussion

In 20 years of continuous forest disturbance from existing and emerging land-use, the MxMBC experienced net forest loss of 2.2%, at an annual deforestation rate of 0.09% (Table 1). Annual deforestation rates during the 20-year period are not constant but variability is consistent with previous work in the region (Turner et al. 2001). Forest regeneration accounts for 0.93% of total forest area in 2020 and contributes to overall forest expansion in the MxMBC in three of seven time intervals, (2007–2010, 2014–2015, 2015–2017) (Table 1, Fig. 3).

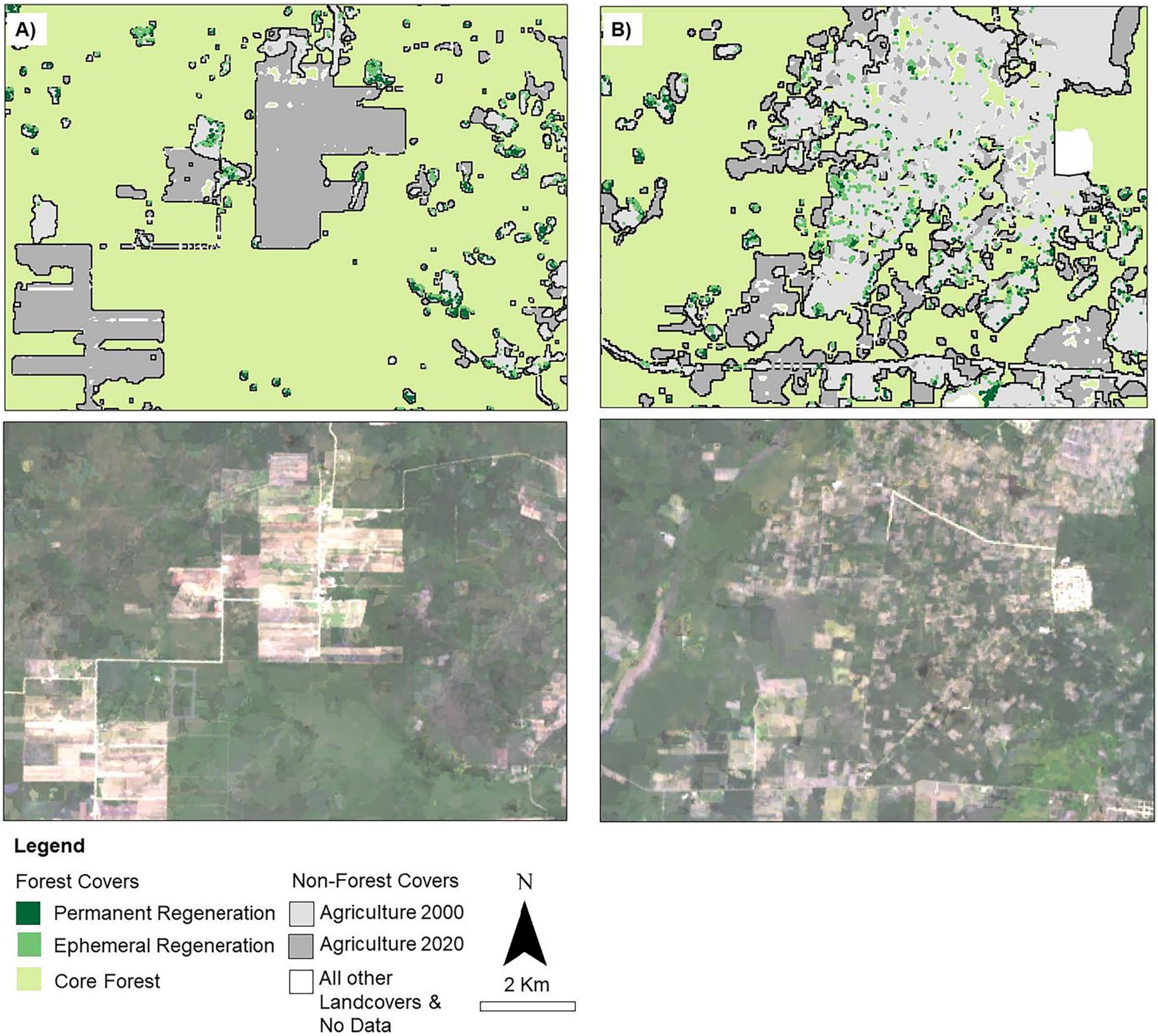

Fig. 4 Patterns of forest regeneration in the MxMBC within complex landscape mosaics of core forest, and agricultural landcovers in both 2000 and 2020. Patterns of permanent and ephemeral forest regeneration are seen widely distributed in small, disparate regenerating forest cover patches across the study site. All landscape regeneration patterns can be found in landscape matrices where large, intensified, agricultural landcovers have expanded into forest core since 2000 (**A**), as well as in landscape matrices where smaller more extensive agricultural land covers have not expanded into forest core since 2000 (**B**). The 2020 Landsat 8 OLI satellite image is shown for both **A** and **B** regions for additional landscape context

While the expansion of MxMBC forest during some intervals in the study period is promising, alongside nearly equivalent annual rates of net proportional forest cover loss and gain over the 20-year study period (SITable 4), research from Brazilian Atlantic forests indicates that loss to local mature forest regions may be masked by the gain of younger regenerating forests (Rosa et al., 2021). Furthermore, studies on the dynamics of regenerating forests have found that regenerating second growth is predominantly ephemeral in both contexts of the Brazilian Amazon (Wang et al. 2020) and Costa Rica in the MBC (Fagan et al. 2013; Reid et al 2018). Examining spatiotemporal patterns of forest regeneration and configuration shows that both permanent and ephemeral patterns of forest regeneration in the MxMBC are associated with the fragmentation of mature core forest and an increase in mean agriculture patch size (Table 2, Fig. 4), indicating that expansion of agricultural plots is not necessarily consolidating land-use or conserving tracts of core forest on the margins of permanent plots. Furthermore, regeneration is positively associated with forest islets, small

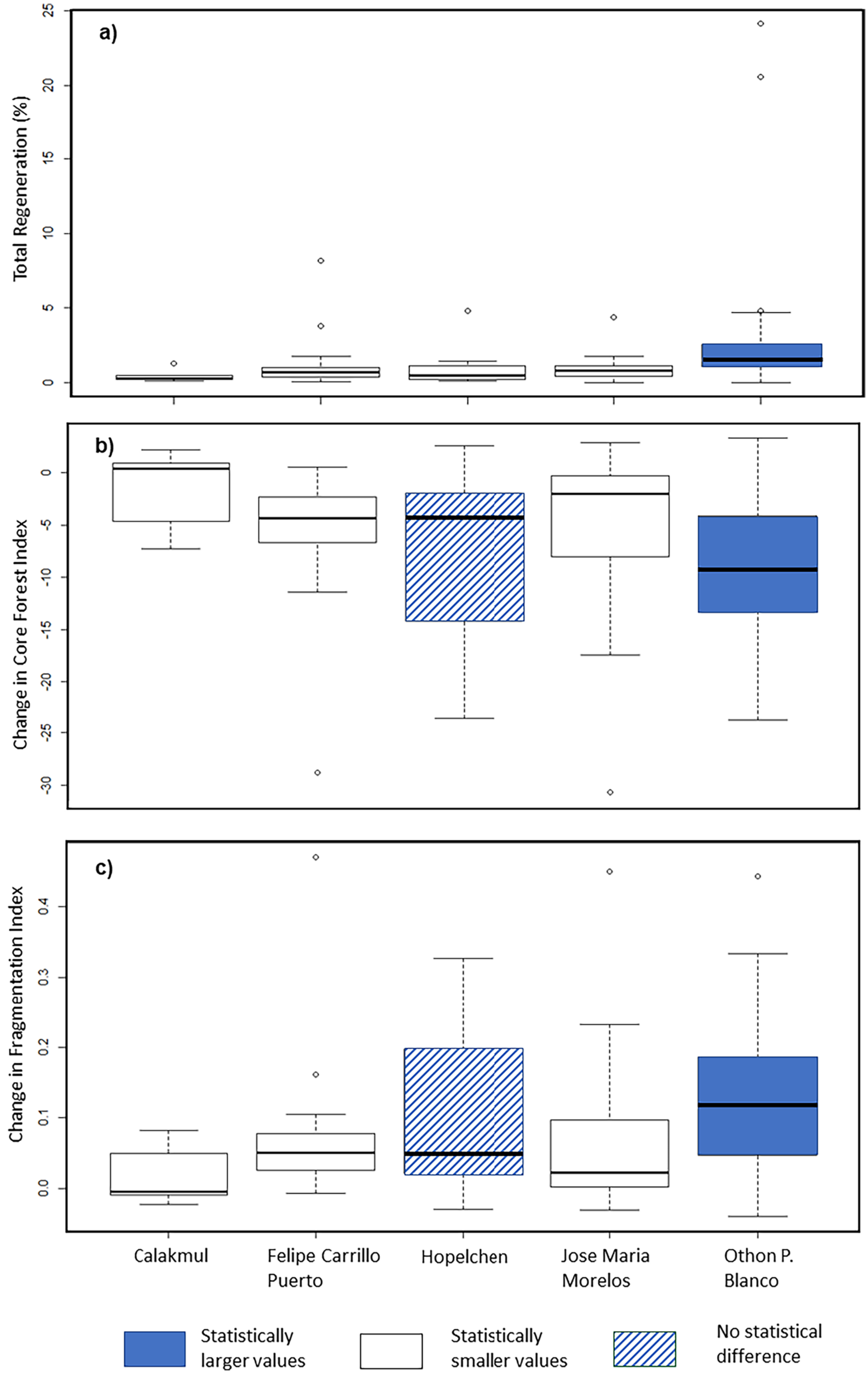

Fig. 5 The distribution statistically significant differences in total forest regeneration and forest configuration indices for *ejidos* of 5 municipalities of the MxMBC. **A** shows statistically larger percentage of total regeneration (permanent, CEA, CMA, and CLA regeneration patterns combined) in *ejidos* of Othón P. Blanco than those of all other municipalities. **B** shows statistically larger changes to core forest index (2000–2020) in *ejidos* of Othón P. Blanco than those of José Maria Morelos, Felipe Carrillo Puerto, and Calakmul. **C** shows statistically larger increases in fragmentation index (2000–2020) in *ejidos* of Othón P. Blanco than those of José Maria Morelos, Felipe Carrillo Puerto, and Calakmul

patches of forest not large enough to be classified as core, and forest perforations, deforestation areas within core forest (Table 2). Together, the relationship of forest regeneration and forest configuration alongside regional examination of these patterns suggest that regenerated forest across the MxMBC contributes to a landscape of small, widely dispersed second growth forest alongside deforestation of core forest within a larger mosaic of land-use and human settlement, following reported regeneration trends across Latin America and the MBC (Rosa et al. 2021; Wang et al. 2020; Reid et al. 2018). This signals that despite the emergence of mechanized cash crop agriculture (Ellis et al. 2017b) and increases in agricultural patch size in some *ejidos* across all municipalities (SITable 6), land left to regenerate following land-uses in the MxMBC does not contribute to conserved regeneration areas separate from human activity, as posed by a land sparing approach. Instead, land-use continues in remaining available forest area, through cycles of fragmentation and subsequent regeneration of small, discontinuous forest patches ranging from permanent to ephemeral. This pattern emerges despite the thresholding process used to refine forest-non forest maps, which removed pixels from analysis that are spectrally similar to the dominant vegetation classes in agricultural working lands, such as pasture or *milpa* land covers, where the process of deforestation and regeneration through land sharing is expected to occur most often.

Spatio-temporal patterns of forest regeneration and configuration in the MxMBC show how the abandonment of land to regenerate alongside permanent cash crop agricultural does not necessarily spare forest cover from future land-use. This follows numerous studies in Latin America that challenge the conservation benefits presented in land sparing approaches (Gutiérrez-Vélez et al. 2011; Ferraz et al. 2014). For example, Rudel et al. (2009) identified that at the global scale, the "sparing" of land around agricultural areas undergoing agricultural intensification occurred in discontinuous spatial patterns that align more with land sharing. A case study in Brazilian Atlantic tropical forests found that expansion into core forest resulted in a fragmented patchwork of regenerated forest patches of multiple ages (Ferraz et al. 2014). Furthermore, an assessment of forest regeneration across the tropics notes that while tropical secondary forest cover can be highly resilient, with regeneration of some old-growth attributes occurring after 20 years, most attributes such as biomass regeneration for carbon sequestration and species compositions can take greater than 100 years to reach levels of old-growth forest (Poorter et al. 2021). While examining composition and structure of regenerating forests was outside the scope of this research, lower deforestation rates in the MxMBC have been recorded in *ejidos* with ongoing cycles of semi-subsistence swidden agriculture or agroforestry and regeneration, although forest degradation in regenerated forest regions from mature old-growth forest compositions and structures still exists (Ellis and Porter-Bolland 2008; Ellis et al. 2017a; Miteva et al. 2019; Poorter et al. 2021). While future studies may look to incorporate plot level variables of regenerating forest composition and structure, as well as spatio-temporal patterns of forest configuration over a larger temporal scale to better assess degradation, the variability of forest regeneration and forest configuration measures in *ejidos* of all five municipalities of the MxMBC (Fig. 5; SITable 6) over the 20-year period in this research points to diverse land management strategies at the level of the *ejido*. As such, examining general land-use contexts behind the spatial patterns of forest regeneration and forest configuration highlight how regeneration maintains forest cover and related environmental processes.

The spatial distributions and patterns of ephemeral CMA and CLA forest regeneration and forest landscape configurations result in two distinct land sharing cases in the MxMBC (Fig. 4). First, regeneration patterns act to buffer clearing of mature forest, as land sharing in areas of semi-subsistence swidden agriculture and agroforestry integrate the process of regeneration as part of regular cultivation cycles (Fig. 4B). Land abandonment and regeneration in semi-subsistence *ejidos* correspond to patterns of both permanent and ephemeral regeneration, where non-forest areas transitioned to forest after 2007 (SITable 6). For example, *ejidos* of Felipe Carrillo Puerto, a municipality with the third highest mean area of all regeneration patterns, but not found to be statistically different from four of the other municipalities in terms of all regeneration patterns had one of the smallest changes to core forest and fragmentation indices, with mean decreases of core forest index and increase in forest fragmentation index values that were half of those recorded in *ejidos* of Othon P. Blanco (Fig. 5; SITable 6). Ellis and Porter-Bolland (2008) found that in the region of Felipe Carrillo Puerto, regrowth and lower deforestation rates correspond to small forest clearings and community-based land management plans that distinguish specific regions for agriculture, timber harvesting, and forest protection at the *ejido* level. As such, ephemeral regeneration may be acting as a deforestation buffer for mature forests, mirroring trends in the Brazilian Amazon where secondary forest loss was driven by a preference for forest clearing in unprotected regions dominated by younger secondary growth (Wang et al. 2020). In the context of regeneration as buffer, ephemeral regeneration in the MxMBC integrates into areas designated for semi-subsistence agriculture and is integral to land-use pathways based on forest cover maintenance with little deforestation (Ellis and Porter-Bolland 2008).

Second, ephemeral CEA, CMA, and CLA regeneration contributes to land sharing in forest areas at the margins of core forest cleared for permanent, mechanized cash crop

Table 2 Spearman's Rank Order correlation Rho values to test for statistically significant correlation between regeneration stages in the study site and forest configuration variables. All presented *rho* values are statistically significant (*P*-value < 0.05)

Consecutiveness	Pattern ID	Proportion core forest		Proportion islet forest		Proportion perforation		Forest fragmentation		Mean non-forest patch size (m)	
		2000	2020	2000	2020	2000	2020	2000	2020	2000	2020
Total regeneration	-	−0.67	−0.45	+0.65	+0.50	+0.63	+0.44	+0.67	+0.45	+0.35	+0.29
Permanent	-	−0.55	−0.24	+0.50	+0.27	+0.49	+0.29	+0.55	+0.24	+0.28	+0.19
Early consecutive	A	−0.63	−0.48	+0.57	+0.48	+0.63	+0.52	+0.63	+0.48	+0.31	+0.26
Middle Consecutive	A	−0.52	−0.42	+0.54	+0.45	+0.53	+0.41	+0.52	+0.42	+0.28	+0.24
Late Consecutive	A	−0.48	−0.28	+0.51	+0.31	+0.43	+0.29	+0.48	+0.28	+0.26	+0.17

cultivation since 2000 (Fig. 5). In these regions with clusters of all regeneration patterns, regeneration is not occurring solely in areas of continuous agriculture but is spatially separated from land cleared since 2000 and emerging in smaller forest islets, effectively masking the loss of core forest and providing opportunity for future land-uses at the margins of mechanized cash crop agriculture (Fig. 5). For example, municipalities of Hopelchén and Othón P. Blanco have the largest mean areas of all regeneration patterns, alongside the two largest mean increases in fragmentation index values, decreases to core forest index, and a wide range of agricultural patch sizes, including the largest increases in mean agricultural patch sizes in Othón P. Blanco (Fig. 5, SITable 6). Ellis and Porter-Boland (2008) found that in Hopelchén, the combined influence of government policies (i.e., PROCAMPO) and land reform in the late 1990s (i.e., PROCEDE) has resulted in increased deforestation through agricultural expansion and intensification into core forest for the cultivation of cash crops, predominantly by groups outside of the *ejido*. Similar patterns of agricultural expansion into core forest are seen in Othón P. Blanco and recorded in an average increase in mean agriculture cover patch size (SITable 6). However, the wide range in changes to mean agricultural patch sizes in ejidos of these two municipalities indicates that in regions of agricultural expansion clearing has not taken the place of traditional land-use such as swidden agriculture (*milpa*). Schmook et al. (2013) note that in *ejidos* of Calakmul, as diverse socio-economic opportunities may decrease individual households' dependency on agricultural production, they also allow households to focus on and maintain *milpa* for subsistence and cultural reproduction. In turn, these areas undergo multiple and potentially compounding pathways of forest use and potential forest regeneration, where forest at the margins of consolidated cash crop cultivation is made available for semi-subsistence swidden agriculture.

Two land sharing contexts in the MxMBC, regeneration as buffer and regeneration as mask, suggest that varying spatio-temporal patterns of forest regeneration have implications for the maintenance of forest cover and subsequent ecosystem processes provided by the forest matrix, due to the relationship between forest regeneration and forest configuration. In regions with semi-subsistence swidden agriculture and agroforestry, characterized predominantly by CMA and CLA regeneration patterns, smaller decreases to forest core maintain a low regeneration to mature forest ratio (Chazdon et al. 2009). Regeneration through land sharing in these regions acts as a buffer to mature forest clearance, sustaining both forest cover (Ellis et al. 2020) and ecosystem processes, such as biodiversity (Melo et al. 2013), biomass regeneration, and related carbon sequestration (Poorter et al. 2016). Alternatively, the connectivity of overall forest cover is reduced in regions of both land sharing through semi-subsistence swidden agriculture and agricultural expansion for cash crop cultivation, characterized by CEA, CMA, and CLA regeneration, as expansion of agriculture into the forest core, spatially separated from areas of forest regeneration, compounds forest fragmentation. Subsequently, smaller regenerated forest patches mask losses of mature forest and contribute to an increasingly fragmented forest matrix that may reduce biomass regeneration and species biodiversity (Ferraz et al. 2014; Edwards et al. 2010; Martin et al. 2013). Furthermore, land sharing through forest regeneration and simultaneous, yet spatially separated, expansion into core forest increases vulnerability of a continually fragmented forest matrix to clearance for agriculture (Schwartz et al. 2017; Reid et al. 2018) and environmental disturbances such as hurricane force winds (McGroddy et al. 2013; Schneider et al. 2016). Taken together, the two land sharing scenarios in the MxMBC, regeneration as buffer and regeneration as mask, show that spatially explicit pattern of forest regeneration and related landscape configurations have implications for the maintenance of ecosystem processes.

Conclusion

The positive relationship of forest regeneration patterns and fragmented forest configurations in the MxMBC suggests that land sharing systems persist. This pattern holds both in the context of traditional land-use of swidden agriculture and agroforestry, where regeneration buffers mature forest from clearance, and alongside recent land-use expansion into core forest, where regeneration masks subsequent forest loss and increasing fragmentation. These two regeneration contexts contribute a framework to understand how regenerating forests patches can maintain forest cover and landscape dynamics across Latin America and the Neotropics, by examining the general land-use contexts behind the spatial patterns of forest regeneration. While specific analysis of forest regeneration in the context of historical land-uses, land tenure, and land governance regimes was outside the realm of this study, previously reported land-use contexts such as those in *ejidos* of Felipe Carrillo Puerto, Hopelchén, and Othón P. Blanco (Ellis and Porter-Bolland 2008; Ellis et al. 2017a, b; Miteva et al. 2019; Ellis et al. 2020) speak to the importance of very local processes, in defining the role of regeneration for the broader socio-ecological forest landscape. Furthermore, small, isolated forest regeneration patches emerge within fragmented forest landscapes despite this research taking place between the Calakmul and Sian Ka'an Biosphere reserves, formal protected areas that can contribute to land sparing through the conservation of primary forests within *ejido* boundaries. These findings support how land sparing, even through formal protected areas, does not necessarily conserve core forest in the MxMBC, as land-use intensification results in increased fragmentation and deforestation of core forest outside the protected area. Taken together, dynamic patterns of regeneration can speak to how different forest configurations are maintained at multiple spatio-temporal scales through a variety of land-use and livelihood strategies, with implications for sustaining environmental processes of the larger forest matrix in the face of continued human and environmental disturbance.

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Declarations

Conflict of interest The authors declare no competing interests.

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