

Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America

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Forest transitions (FT) have been observed in many developed countries and more recently in the developing world. However, our knowledge of FT from tropical regions is mostly derived from case studies from within a particular country, making it difficult to generalize findings across larger regions. Here we overcome these difficulties by conducting a recent (2001–2010) satellite-based analysis of trends in forest cover across Central America, stratified by biomes, which we related to socioeconomic variables associated with human development. Results show a net decrease of woody vegetation resulting from 12,201 km² of deforestation of moist forests and 6,825 km² of regrowth of conifer and dry forests. The Human Development Index was the socioeconomic variable best associated with forest cover change. The least-developed countries, Nicaragua and Guatemala, experienced both rapid deforestation of moist forests and significant recovery of conifer and dry forests. In contrast, the most developed countries, Panama and Costa Rica, had net woody vegetation gain and a more stable forest cover configuration. These results imply a good agreement with FT predictions of forest change in relation to socioeconomic development, but strong asymmetry in rates and directions of change largely dependent upon the biome where change is occurring. The FT model should be refined by incorporating ecological and socioeconomic heterogeneity, particularly in multicountry and regional studies. These asymmetric patterns of forest change should be evaluated when developing strategies for conserving biodiversity and environmental services.

land-use change | land-cover change | tropics | Latin America

Deforestation and forest degradation are among the world's most pressing land-change problems. Between 2000 and 2010, there was an estimated global net loss of 521,080 km² in forest cover (1), an area about the size of Central America. However, in many regions, forest cover is expanding, following a land-change pathway known as forest transition (FT) (2). In its simplest form, FT has been defined as a shift or “transition” from net deforestation to net forest regrowth for a particular country or region, but in actuality FT implies a gradual “pathway” of change instead of threshold or a specific turning point (3). In the early stages of a country's development, forest area declines because of expanding agricultural activity; in later stages, it gives way to net forest recovery because of a combination of factors, and finally the rate of change slows down, tending toward a relatively stable land-cover configuration (Fig. 1A). Along this hypothetical pathway there are periods of rapid net forest change (i.e., when deforestation or reforestation clearly dominate), and periods when net change approaches zero, in the turning point from net deforestation to net reforestation and at the final stabilization stage (Fig. 1B).

A salient feature of FT is its theoretical association with socioeconomic development and globalization (4–6), which implies that advanced levels of development can be compatible with certain levels of forest conservation and recovery. Changes in forest cover have major ecological consequences by directly affecting biodiversity, carbon budget, and soil and watershed

conservation (7). Therefore, understanding patterns and drivers of forest change and possible FT trajectories is relevant to a broader societal goal of achieving land-use sustainability in the face of rapid global environmental and socioeconomic change.

Recent studies suggest that FT is associated with variables related to socioeconomic development, such as rural abandonment and accompanying urbanization, agricultural intensification, the establishment of extensive tree plantations (often through state-driven policies), economic industrialization, growing education and technical knowledge, and the strengthening of sociopolitical institutions (8–20). However, these studies, including the seminal descriptions of FT in Europe (21–25) and Southeast Asia (10, 26), are mostly derived from case studies of a single country, usually because data are only available at the national level, which limits the potential for broad-scale extrapolation or generalization of findings and has strong potential for biases because of arbitrary or opportunistic site selection (27). Largely overlooked is the fact that countries include significant environmental heterogeneity within their borders, with multiple biomes and forest types that differ in size, location, distribution, and ecological characteristics. Typical comparisons based on previously published material usually do not discriminate among forest types and instead focus on “forests” as an implicitly homogenous category, thereby ignoring forest variation and its effect on the spatial partitioning of ecological and socioeconomic processes.

This study overcomes these limitations by conducting a recent (2001–2010) satellite-based, quantitative analysis of trends in forest cover in the seven countries that comprise Central America. We addressed the environmental heterogeneity found across this region by including analyses at the biome level within each country, and then relating patterns of forest change with national socioeconomic variables associated with human development. Several reasons make Central America a compelling region for a multinational analysis that relates forest trends with socioeconomic development. First, the region comprises seven countries that share important cultural features and have a similar physical geography characterized by high biodiversity and strong ecological gradients associated with the volcanic mountain chain, which separates moist forests on the Caribbean, dry forests on the Pacific, and cooler montane forests in the highlands (including conifers in the north). Second, during the past few decades, the region experienced major changes associated with socioeconomic globalization, including strong increases in foreign investment, establishment of international free-trade agreements, and strong

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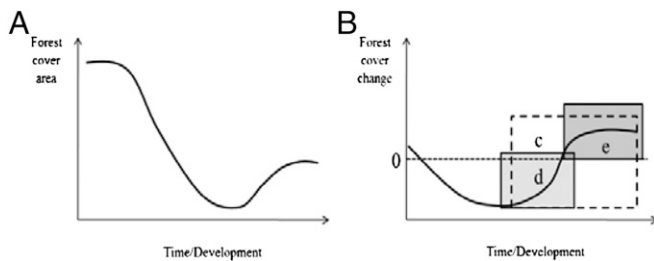


Fig. 1. Hypothetical pathway of forest cover (A) and forest cover change (B) in the Forest Transition Model. Subboxes in B indicate the stage found in this study for Central American countries: (c) whole countries, (d) moist forest life zones, (e) Conifer and Dry forest biomes. The y axis of the figures are not scaled because absolute values can vary among countries.

migration to developed countries (particularly to the United States), with resulting economic inputs in the form of remittances and tourism development. These effects, however, vary significantly among the different countries because of their differing levels of socioeconomic development spanning a range similar to that observed across Latin America. Thus, Central America provides an excellent opportunity to assess land cover change along a representative gradient of development.

Central America experienced rapid deforestation during the 20th century, particularly between the 1960s and 1980s, but more recently several local case studies have shown forest recovery. The most recent review of forest trends in Central America (28) concluded that, although there is room for “cautious optimism” in the sense that the region could follow a FT pathway; the patterns are unclear and limited by the lack of up-to-date forest monitoring. Studies of land change in Central America and other regions in Latin America have identified many socioeconomic factors favoring forest recovery, including: international remittances (29–31), migration (32–35), urban/rural population change (36–39), rural abandonment and accompanying urbanization and industrialization (18, 35, 40), foreign investment (41), tourism (4), establishment of protected areas (42, 43), expansion of shade coffee oriented to global markets (27), establishment of tree plantations (17), and growth of the services economy (44, 45). These studies, however, are mostly restricted to one country or a subnational area, and do not discriminate among forest types or ecological subnational regions. In addition, all but a few of these studies are outdated because only one national-scale analysis (46) employs imagery after 2000.

In this study we tested the general hypothesis that Central America is following a FT pathway associated with socioeconomic development during the past decade, and that national trends are influenced by ecological heterogeneity, which produces a complex dynamic of land-cover trajectories. To explore this general hypothesis in detail, we focused on the following objectives: (i) Compare trends in forest cover during the last decade across the different countries and major biomes (moist forest, conifer forest, dry forest) in Central America; and (ii) Determine the relative importance of socioeconomic variables [e.g., population, remittances, foreign investment, human development, gross domestic product (GDP), migration, and poverty] in explaining the patterns of forest cover change.

Results

Geographic Patterns of Forest Cover Change. From 2001 to 2010, Central America experienced a net loss of 5,376 km² of woody vegetation (trees and shrubs covering at least 80% of the pixel). Percent of forest cover remaining at the end of the study period in decreasing order was: Belize (63%), Costa Rica (46%), Panama (45%), Honduras (41%), Guatemala (37%), Nicaragua (29%), and El Salvador (21%). In addition, trends in forest change

varied among biomes (Fig. S1). The moist forest biome experienced a net loss of 12,201 km² and more than 99% of woody vegetation loss occurred in this biome. Forest loss was partially offset by a net gain of 6,825 km² of woody vegetation in the coniferous (+4,730 km²) and dry (+2,054 km²) forest biomes. Mangroves and Deserts showed net woody vegetation loss and gain, respectively, but their relative contribution to regional woody change was less than 1%; thus, we focus on results from the moist forest, dry forest, and coniferous forest biomes.

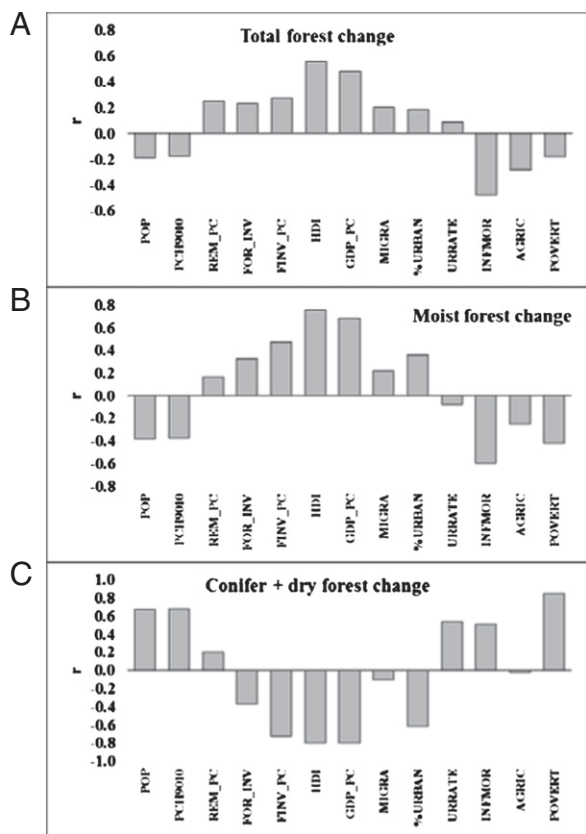
In the moist forest biome, deforestation mainly occurred along the Caribbean slopes of Nicaragua (−8,574 km²), Guatemala (−4,816 km²), and Honduras (−263 km²) (Figs. S1 and S2). Deforestation “hotspots” were concentrated along Nicaragua’s northeastern Atlantic coast, northern Guatemala’s Petén, and the Olancho and Mosquitia regions of northeastern Honduras (Table S1). Belize lost 47 km² in the moist forest biome, and El Salvador and Panama experienced small net gains in moist forest biome (+44 km² and +31 km², respectively). Costa Rica was the only country that had substantial gains (+1,477 km²) in the moist forest biome, largely near the borders with Panama and Nicaragua and in the central highlands (Table S1).

Forest regrowth dominated the coniferous forest and dry forest biomes (Figs. S1 and S2), particularly in Honduras (+3,050 km² and +673 km², respectively), Nicaragua (+954 km² in dry forests), Costa Rica (+151 km² in dry forests), and El Salvador (+360 km² and +183 km², respectively). No municipality gained more than 500 km² of woody vegetation (Table S2). Areas of regrowth were more dispersed than areas of deforestation, although two general clusters emerge: (i) the highlands of the Central America Volcanic Axis of Guatemala, Honduras, El Salvador, and Nicaragua; and (ii) the Pacific coastline of Nicaragua, Costa Rica, and Panama. Deforestation in conifer and dry forest biomes was negligible. Only Nicaragua’s conifer forest experienced overall net deforestation (−352 km²), but this was because of forest loss in two municipalities where conifer forests occur at low elevation, adjacent to a hot spot of deforestation in the moist forest biome in the northeastern Atlantic coast. Most of the other municipalities in coniferous forest biome occur in the uplands of northwest Nicaragua, and they experienced expansion of woody cover.

Relationship Between Forest Trends and Socioeconomic Variables.

The Human Development Index (HDI) was the variable with the greatest linear correlation with net total forest change (Fig. 2A). In general, variables positively associated with development—HDI, GDP per capita, foreign investment per capita, international migration rate, percentage of urban population, urbanization rate, and remittances per capita—were correlated with forest gains; whereas social and demographic variables mostly associated with lower levels of development—infant mortality, percentage of population below poverty line, country population, population change between 1990 and 2010—were correlated with forest losses. Associations with moist forest change show the same general pattern as with total forest (Fig. 2B), whereas dry and conifer forest expansion was positively correlated with a country’s population and poverty level, and was negatively correlated with HDI and GDP, indicating that net forest regrowth was more active in countries with lower levels of development (Fig. 2C).

Overall forest trends across Central American countries are consistent with the FT model (Fig. 1B). Although the relationship was not statistically significant, there was a general tendency for less-developed countries, such as Guatemala and Nicaragua, to be dominated by net deforestation, but the more developed countries, such as Costa Rica and Panama, experienced net woody vegetation recovery (Fig. S3A). Honduras showed a more advanced stage of FT than expected based on its level of HDI. Although El Salvador and Belize share a similar level of development, their forest trends differ in association with their dominant biomes: Belize (moist forests, Atlantic coast) experienced



POP country population in 2010
 PCH9010 population change between 1990 and 2010
 REM_PC remittances per capita in 2009
 FOR_INV total foreign investment in 2010
 FINV_PC foreign investment per capita in 2010
 HDI Human Development Index for 2010
 GDP_PC GDP per capita in 2010
 MIGRA international migration rate in 2010
 %URBAN percentage of urban population in 2010
 URRATE urbanization rate in 2010-2015
 INFMR infant mortality in 2010
 AGRIC percentage of agricultural GDP over total GDP in 2006
 POVERT percent of population below poverty line in 2010

Fig. 2. Correlation coefficient between country level socio-economic variables and types of forest cover change: (A) total forest change; (B) moist forest change; and (C) conifer and dry forest change.

net deforestation, and El Salvador (conifer and dry forest, Pacific) experienced net forest regrowth. The positive correlation between country HDI and forest change was stronger and statistically significant ($r^2 = 0.71$) for the moist forest biome (Fig. S3B). In contrast, the association between HDI and forest change in combined dry and conifer forests was slightly negative ($r^2 = 0.13$), which despite the small sample size for a correlation analysis, suggests that less-developed countries in Central America not only tend to show more deforestation in the moist forest biome, but they also tend to recover more dry and conifer forests (Fig. S3C). As a result of the patterns of deforestation and regrowth in relation to HDI (less-developed countries experienced both more deforestation and regrowth), there is a statistically significant negative correlation between “forest instability” (an index of country-scale change in forest distribution) and HDI (Fig. S3D).

Discussion

FT Model in Central America. Central America as a whole is not undergoing a net forest recovery. However, when the countries

are ordered according to their level of socioeconomic development, trends in forest cover change are consistent with the predictions of the FT model (Fig. 1C, box c, and Fig. S3A), in which less-developed countries (Guatemala, Nicaragua, present study) are at a stage of net deforestation, and more developed countries (Panama, Costa Rica) experienced net forest recovery.

Our study goes beyond case studies and informal comparisons to present quantitative evidence of the association between FT and socioeconomic development using a multinational approach. Potential mechanisms behind these trends involve different factors derived from socioeconomic development including: (i) more efficient protected areas financed by stronger economies and by their association with international cooperation and tourism (47, 48); (ii) higher social perception of the benefits of preserving forests as a source of environmental services, likely associated with higher education levels (2); (iii) decreasing importance of low-input land uses (particularly extensive cattle ranching) in favor of more intensive agriculture that could promote “land-sparing” mechanisms [e.g., Costa Rica (49)] or non-agriculture economic activities [e.g., Panama (47)]; (iv) stronger institutions to regulate land uses in more developed countries (50); and (v) a less-institutionalized land-tenure system in less-developed countries, which makes it theoretically possible to engage in larger land acquisitions and may lead to larger out-migration streams.

The relationship between national development and country-scale forest cover trends hides major differences within countries that emerge when forest cover is analyzed at the biome level, which are also associated with different levels of development. The moist forest biome, particularly in the Caribbean lowlands, experienced rapid deforestation in the less-developed countries, but the two most-developed countries experienced forest regrowth, as predicted by the conceptual FT model (Fig. S3B). In contrast, high-elevation conifer and Pacific dry forests tended to have increasing forest cover, which decrease in intensity with development level (Fig. S3C). As a result of these contrasting trends related to ecological heterogeneity and a spectrum of intranational development, less-developed countries experienced significant more forest instability and forest redistribution at the country scale because greater HDI was associated with more stable forest cover (Fig. S3D). This trend toward forest stabilization can also be explained by the FT model, especially when considering the different levels of development at the subnational level. Overall, the moist forest zones of Central America, largely located in the Caribbean slope, have lagged behind in the development history of the different countries, a situation that dates back to the pre-Colombian era when settlement was concentrated in the highlands and the Pacific slope (47, 51–54). In the FT models, moist forests would fit in the stage at which less-developed countries, such as Nicaragua and Guatemala, have rapid deforestation, whereas more-developed countries, like Panama and Costa Rica, show incipient patterns of regrowth (Fig. 1B, box d). In contrast, the dry and conifer forest zones of comparatively more-developed countries show a more advanced stage in the FT model (i.e., when forest dynamics transition from forest expansion to a period of stability and little change) (Fig. 1B, box e). In summary, there is an asynchronous behavior of forest cover change across biomes, with both faster deforestation (in moist forests) and regrowth (in dry and conifer forests) trends in less-developed countries (Fig. S3D).

This study is unique in showing a multinational association between country development and forest trends in a tropical region, with countries sharing comparable cultural and biophysical characteristics. The quantitative associations between forest trends and development should not be directly extrapolated to countries with different ecological characteristics or cultural settings, and the similarities among Central American countries should not be overemphasized (Panama and Costa Rica do not have conifer forests and Belize does not have dry forests).

However, the general pattern of distinctive land uses between the highlands and the Pacific and Caribbean slopes provided an overall comparative framework. As a result, we were able to add two significant contributions to the study of FT. First, HDI emerges as the most important predictor of forest cover change in our study. Within the range of HDI in Central America, countries tend to change from net deforestation to net forest recovery as HDI increases. This pattern provides evidence of a consistent association between development and land-use trends leading to FT, and the fact that HDI has a stronger correlation with FT than the other single variables analyzed suggests that there are different components of socioeconomic development that contribute to FT. Second, forest change has clear sub-national geographic patterns with a strong asymmetry between biomes. The reason behind these differences may be because of the fact that the conifer and dry forests of the highlands and Pacific coast have a much longer colonization history, more developed socioeconomic conditions and, as a result, relatively less remaining land to deforest. This issue is further compounded by a lack of enforcement of land tenure in the less-developed countries (e.g., ranchers moving onto indigenous lands in Mosquitia in Honduras and Nicaragua). The result of this asymmetry is that less-developed countries have more dynamic forest cover, with intense deforestation and regrowth processes in different biomes. More-developed countries have a more stable forest cover configuration, a scenario less-developed countries could be heading toward. This asymmetry involves significant ecological consequences and indicates that there are complex driving forces of forest change operating at subnational scales, partially constrained by environmental conditions. A major consequence of this pattern for land-use management and policy is that, although less-developed countries need urgent actions to protect the most valuable areas of rainforests (55), they also offer the greatest possibilities for ecological restoration of conifer and dry forests (56, 57).

Proximate Forces of Deforestation and Regrowth. The net loss in forest cover across the region is a result of the rapid deforestation in the Caribbean moist forests of the less-developed countries. These are areas that have shown increasing agriculture area from 2001 to 2010. For Guatemala, Nicaragua, and Belize, our data show that agricultural/herbaceous vegetation increased by 6,866 km². Between 1966 and 1994, Guatemala lost 22% of its forest cover to agricultural settlement (~7% per decade), mainly in the north (58), and we found this trend has continued during the past decade, with a total loss of 7% (3,019 km²). It is also worthwhile to note that similar patterns are also found in neighboring areas of the Yucatan, thereby extending the area of this deforestation hotspot (59). Because the latter 7% is over a smaller, total remaining area, the absolute forest change rate appears to be slowly decreasing, thus further supporting the idea that Guatemala indeed fits into Fig. 1B, box c. In northern Guatemala, deforestation is associated with distance to human settlements (60) and rapid population growth (from 1.9 million to over 3 million in the four northern departments), factors related to forest conversion for subsistence maize farming and pasture creation (61). Agricultural data from the Food and Agricultural Organizations of the United Nations (62) supports this claim by showing that from 2001 to 2008, the area under maize, sugarcane, and bananas increased by 3,581 km² for all of Guatemala. Nicaragua experienced the highest decadal deforestation rate, with a loss of 7,961 km² of forest during the last 10 y. Although socioeconomic drivers of deforestation in Nicaragua may be similar to those in Guatemala, national statistics (62) and previous studies (63) suggest that a much lower proportion of deforested areas go to agriculture, which may imply they are mostly converted into extensive pastures.

Forest regrowth, on the other hand, is a result of secondary succession following agricultural and pastureland abandonment.

In Honduras and El Salvador, the area under agricultural and herbaceous cover declined overall by a total 2,335 km² from 2001 to 2010, and in general, areas of agriculture decline coincide with areas of forest recovery. The largest losses among crops were, in order of magnitude, sorghum, maize, and cocoa (62). These losses were largely concentrated in the intermontane valleys and the Pacific highlands of conifer and dry forest biomes. In contrast, gains among crops were, in order of magnitude, sugar, coffee, and rice, concentrated along Honduras's north coast and into Mosquitia. In Panama, the area under land-use also declined and was mainly attributed to the loss of rice, maize, and bananas (62). Of the four countries with net forest regrowth, Costa Rica was the only one with increases in cropland area (present study and ref. 62); coffee, oranges, and maize decreased in area, but this was outweighed by gains in sugarcane, fresh fruit, and rice.

Agricultural area has declined in three of the countries with regrowth (present study and ref. 62). This decline may be beneficial for local natural ecosystems; however, as a country's population grows and agriculture declines, its reliance on food imports increases, which may imply the transfer of agriculture pressure to ecosystems in other parts of the world (64). Much of the agriculture declines in Central America have occurred at the expense of subsistence crops, such as maize, beans (or sorghum), and squash—the staples of the regional diet—and is being replaced by cash crops, such as sugarcane, bananas, and coffee. In six of the seven countries in Central America (Panama being the exception), sugarcane was one of the top three crops that gained in area from 2001 to 2008; maize, on the other hand, was one of the top three crops that lost area during the same time period in four countries (62).

Drivers of forest expansion appear to involve different mechanisms related to the level of development. In the most-developed countries, such as Costa Rica (which had a relatively high deforestation rate only two decades ago), efficient protected areas, such as the Guanacaste Conservation Area, have been instrumental in favoring dry forest recovery (57) and preventing further deforestation in moist forests (48). Similarly, Panama has also reversed its historical deforestation trend (47). Today, protected areas cover 21% of Costa Rica and 19% of Panama (48, 65). Costa Rica has also initiated policies to promote reforestation and forest management (66) including, since 1996, the “polluters pay principle” through a fuel tax, which is used to promote reforestation and conservation activities.

In contrast, in the less-developed countries, the return of forest is probably more related to mechanisms less directly related to government policies, such as human out-migration and the impact of remittances, with El Salvador as a well-studied example. Despite early claims that “nature had already been extinguished in El Salvador” (67), more recent and nuanced analyses (29–31), have shown that some primary forests persist and hundreds of square kilometers of secondary forest have grown back. Our study supports these results by showing that woody vegetation has increased by 16% (586 km²) from 2001 to 2010. The gains we found are comparable to the 22% increase found during the 1990s and early 2000s (30), attributed to the mass exodus of Salvadorians during the 1980s and 1990s, and the remittances sent by these migrants to relatives remaining in El Salvador, which no longer need to cultivate marginal agriculture lands for subsistence.

In addition to reforestation through secondary succession, increases in woody cover can be attributed to shade coffee, particularly in southern and western Honduras. In 2008, coffee represented 32% of the total area harvested in Honduras, and coffee in the uplands has nearly taken precedence over growing traditional staple crops (68, 69). Cultivation of traditional shade-grown coffee, the main cash crop in western Honduras, leaves parts of the original forest canopy or shade trees planted. A substantial portion of the “regrowth,” which occurred in south-

central Honduras during the 1990s, can be attributed to the planting of trees for shade-grown coffee cultivation (27, 70), and this process has likely continued into the last decade.

Conclusions and Implications for Forest Conservation. The analysis of land cover change in Central America during the past decade provides an excellent example of the association between socioeconomic development and forest cover change. Although undoubtedly there are distal transnational influences on land-use change that are not captured by development indices, we were able to conduct a quantitative and updated multinational comparison that generally supported the FT model at a macro scale, and provided a deeper understanding of FT complexities by showing the importance of environmental heterogeneity in influencing patterns of forest cover change, with implications for a country's overall FT pathway. Our results showed that environmental differences between the Caribbean slope and lowlands (moist forests), the uplands (conifer forests in the north), and the Pacific slope (dry forests) of Central America were related to historical differences in development and resulted in a strong asymmetry in the FT pathway, and an overall trend toward forest cover stabilization in more developed countries.

This asymmetry has implications both for the refinement of the FT model and its socioeconomic drivers, and for understanding the consequences of forest cover change in relation to socioeconomic development and globalization. The FT model should incorporate ecological and socioeconomic heterogeneity, particularly in multicountry and regional studies where, as is usually the case, ecological heterogeneity is associated with differences in socioeconomic development. Furthermore, the model could be enriched if statistics on socioeconomic indicators were available at the municipal level.

There are also practical implications of these asymmetric patterns of forest change that should be evaluated when developing strategies for conserving biodiversity and environmental services. After decades of rapid deforestation the most developed countries (Panama, Costa Rica) showed an increase in woody vegetation and they have a relatively stable land cover configuration, with approximately 40% of the country covered by forests. These values are significantly higher than the global average (approximately 30%) and similar to the values in Europe (1) after many decades of forest expansion (2). However, these figures vary greatly and rapidly deforesting countries, such as Guatemala and Nicaragua, already have forest cover below these percentages, suggesting that forest cover may reach percentages as low as the 20% of El Salvador. In addition, "forest" is not a homogenous category and each biome experiences different rates and trajectories of land

change because of different socioecological factors. Current forest loss in Central America is mainly occurring in the moist forest biome, with higher levels of biodiversity in comparison with the recovering regions in the conifer and dry forest biomes. On the one hand, deforestation in the moist forest is not only eliminating high biodiversity habitat, but is also interrupting the connectivity of the "Mesoamerican Biological Corridor," which implies that current forest losses in Central America may be having a disproportionately negative effect on biodiversity. On the other hand, the long history of deforestation and land use in the conifer, and particularly the dry forest biomes, has severely threatened the biodiversity in these regions. Therefore, the current trends of forest recovery should be helping to reduce any further biodiversity loss, and possibly allow wildlife populations to recover.

Materials and Methods

MODIS MOD13Q1 imagery was used to map land-use and land-cover trends (71, 72). Reference data for classifier training and accuracy assessment were collected, with human interpretation of high-resolution imagery in Google Earth using a Web-based tool called VIEW-IT (Virtual Interpretation of Earth Web-Interface Tool) (72). The VIEW-IT tool uses a GE plug-in to allow users to visually estimate percent cover of land-use and land-cover within a sample grid defined by a 250 m MODIS pixel overlaid on high-resolution GE satellite imagery. A total of 4,560 samples were placed only in areas with high-resolution QuickBird imagery, with locations selected both randomly and manually within patch types for the corresponding land-cover classes (72). This classification procedure resulted in land-change maps with eight classes for each year from 2001 to 2010. Average overall accuracy for the three biome maps that covered Central America was 85.1%. For the purposes of this study, only the woody vegetation (trees and shrubs that cover greater than or equal to 80% of the pixel) and agricultural/herbaceous (annual crop, grasslands, and pastures where cover is greater than 80%) classes were used. We focused mainly on trends in the woody vegetation class, as it represents change associated with natural vegetation, such as deforestation or reforestation, which has important implications for species habitat use, carbon dynamics, and FT theory. For a full description of the classification procedure and explanation of Random Forest classification, see *SI Materials and Methods*.

To relate land-cover change with socioeconomic variables, we used Pearson product-moment correlation coefficients between the country level measures and the aggregated net forest cover change during the 10-y period. We show three measures of relative forest cover change by dividing the area of forest cover change by country area: (i) relative total forest change, (ii) moist forest cover, and (iii) forest cover in dry + coniferous forests. These variables were regressed against the several socioeconomic variables, which are listed and explained in full detail in the *SI Materials and Methods*.

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