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On the hope for biodiversity-friendly tropical landscapes

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With the decreasing affordability of protecting large blocks of pristine tropical forests, ecologists have staked their hopes on the management of human-modified landscapes (HMLs) to conserve tropical biodiversity. Here, we examine key forces affecting the dynamics of HMLs, and propose a framework connecting human disturbances, land use, and prospects for both tropical biodiversity and ecosystem services. We question the forest transition as a worldwide source of new secondary forest; the role played by regenerating (secondary) forest for biodiversity conservation, and the resilience of HMLs. We then offer a conceptual model describing potential successional trajectories among four major landscape types (natural, conservation, functional, and degraded) and highlight the potential implications of our model in terms of research agendas and conservation planning.

Conservation out of the wild

To date, conservation strategies for tropical biodiversity have often been based on safeguarding large 'intact' tropical forest reserves. Although recommended [1], this conservation target is proving to be increasingly challenging [2]. Creation of new mega-reserves will soon be severely constrained because most tropical regions already lack large blocks of pristine forest available for conversion into conservation areas [3]. Therefore, the management of HMLs (see Figure I in Box 1) has emerged as a potential opportunity to conserve biodiversity, by creating landscapes where productive lands coexist with natural forests and where biodiversity is conserved by promoting sustainable, nondegrading, agricultural practices [4–8]. These HMLs also include millions of hectares of forests worldwide that are, or will be in the future, selectively logged [9]. They also include the expected expansion of secondary forests in response to the abandonment of agriculturally unproductive lands, which has fueled the notion, by some, that forest gains through regrowth will mitigate or even reverse the current trend of forest loss and degradation [10]. Therefore, it is not surprising that the conservation value of disturbed landscapes has been intensively assessed and the notion that it could serve as a sort of 'Noah's Ark' for tropical biodiversity has been disseminated over both academic and conservation forums [5,11,12].

However, the real potential for biodiversity persistence in such altered landscapes remains unclear and controversial; it is particularly unclear how much, and for how long, tropical biodiversity can persist in HMLs under current land uses [13]. Several studies have reported that small forest patches dominated by second-growth vegetation or biodiversity-friendly crops [14] in HMLs are able to retain high levels of biodiversity of several taxa, including birds [15], mammals [16], and vascular plants [17]. Beyond species diversity, phylogenetic diversity, which helps to understand both the biogeographic history of biological communities and how they are structured [18], is reported to be maintained at high levels for trees in highly fragmented and selectively logged tropical landscapes [19]. Ecosystem services, such as carbon storage and a sustainable water supply, have also been shown to be delivered to human populations even in altered landscapes where native diversity has declined and exotic species have been introduced, creating 'novel ecosystems' [20]. Conversely, studies at large spatial scales have questioned the perception that HMLs are able to retain tropical biodiversity in the long run, especially species that are sensitive to anthropogenic changes [21–23]. Studies addressing the factors that affect the conservation value of HMLs, such as deforestation and fragmentation thresholds, matrix harshness, intensity and type of human-caused disturbances, and land-use dynamics, have detected synergisms among these factors, indicating that biodiversity persistence in altered landscapes is highly variable and context dependent [5,24,25].

The need for a new framework

In summary, the idea that HMLs can harbor high levels of biodiversity and provide ecosystem services to humans is comforting, but there is no consensus on, or even guesses at, the amount of forest [24], the management practices [11,26,27], or the landscape configurations [28] that would ensure the long-term persistence of biodiversity and provision of ecosystem services. Given this, there is a danger that we exaggerate the role played by HMLs in safeguarding tropical biodiversity by considering them, *a priori*, as potentially 'biodiversity-friendly landscapes' [8]. To move forward, we need a conceptual framework that poses working hypotheses, and subsequent verification of those

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Box 1. Tropical HMLs

Imagine any tropical landscape at any spatial scale: lots of forest remnants mostly isolated and disconnected, varying in size, shape, and successional stages, where some native species have disappeared whereas other exotic species have become established. Intense selective logging has depleted the tree biomass and collapsed the forest structure, and overhunting has severely reduced populations of most large-bodied (>1 kg) vertebrates. Edge effects continue to drive microclimatic alterations and surface fires in remaining forests are frequent. Surrounding these forest remnants are cattle ranches, soybean, sugarcane, or palm-oil plantations, and sometimes urbanized human settlements. High-quality forest habitats are increasingly rare and generalist species proliferate in forest edges dominated by secondary vegetation.

Little to no legal protection of the natural habitat leads to uncertainty about the ultimate configuration of such tropical landscapes and, in the best-case scenario, the landscape remains as described above. Such a hypothetical scenario defines HMLs and represents the main configuration of many tropical forests worldwide, such as the Brazilian Atlantic Forest (Figure I), and forests in Madagascar, Indonesia, and India. Except for the Amazon and Congo basins, as well as some islands of Oceania, most tropical forests are as described above or will soon approach this configuration under current land-use patterns.

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Figure I. Aerial perspective of an aging (>100 years) typical tropical human-modified landscape (HML) in Alagoas State, northeast Brazil. Note that sugarcane plantations now dominate where degraded tropical forests cover less than 30% of the landscape. Reproduced, with permission, from Centro de Pesquisas Ambientais do Nordeste and Adriano Gambarini.

hypotheses across multiple tropical regions and sociobiological contexts. Such a framework will: (i) reduce uncertainties; (ii) identify potentially misleading expectations; and (iii) support an effective approach to incorporating HMLs into the conservation agenda.

Here, we examine some of the key forces affecting the nature and dynamics of HMLs, and propose a basic framework connecting human disturbances, land use, and prospects for both tropical biodiversity and human-relevant ecosystem services. First, we question common assumptions of: (i) the forest transition as a worldwide source of new secondary forest; (ii) the role played by regenerating forest (hereafter secondary forest) for biodiversity conservation; and (iii) biodiversity resilience in many HMLs. Second, we capture the main forces acting in the context of HMLs, which set human-disturbance thresholds for both ecosystem services provision and biodiversity persistence. Third, we offer a conceptual model describing potential successional trajectories to be experienced by HMLs in response to patterns of land use and protection of forests. Finally, we highlight the potential implications of our trajectory model in terms of research agendas and conservation planning.

Forest transition questioned

Economic growth, rural exodus, and urbanization are often correlated and represent a widespread and historical phenomenon that results in the abandonment of agricultural lands, particularly those considered marginally productive [29]. In this context, a huge amount of land has been predicted to be available for natural forest regeneration in many tropical countries as long as their economies become increasingly industrialized [30]. This phenomenon, known as 'forest transition' (i.e., the transition from net forest loss to net forest gain), has generated some optimism among conservation biologists. For example, Wright and Muller-Landau [31] stated that: 'Current human demographic trends, including slowing population growth and intense urbanization, give reason to hope that deforestation will slow, natural forest regeneration through secondary succession will accelerate…'. Therefore, one would expect that mixed landscapes (i.e., forest and croplands) will naturally emerge across developing tropical countries in a win-win process where both the economy and biodiversity will benefit from the forest transition process.

Although the movement of human populations from rural to urban areas persists as a current demographic trend, the ultimate fate of abandoned lands is not necessarily the emergence of secondary forests as predicted by the forest transition model [32]. In fact, agricultural expansion is still the main source of tropical deforestation [33]. From 1980 to 2000, up to 80% of global agricultural expansion either was based on newly deforested lands (mature forests) or occurred at the expense of regenerating secondary forests in traditional agricultural lands [34]. Furthermore, recent studies demonstrate that some tropical countries currently experiencing forest transition have increased their imports of commodities, thus exporting deforestation to other countries [32]. Even documented increases in forest cover might comprise species-poor plantations of non-native pulpwood trees (e.g., *Eucalyptus* and *Pinus*) instead of regeneration of biodiverse native forests [35]. By 2005 in China and Vietnam, 16% and 21%, respectively, of all 'forests' comprised tree plantations grown for commercial purposes [36]. As human populations grow, and per-capita consumption of natural resources increases, there is no reason to expect that abandoned lands will turn into long-lasting forest patches as a natural consequence of urbanization [37].

Uncertainties of forest transition: the case of the Brazilian Atlantic Forest

The historical and current land-use trajectory in the Brazilian Atlantic Forest region (BAF) illustrates the uncertainties associated with the predictions of forest transition. The BAF case particularly highlights the weak relation between urban migration and opportunities for forest protection or recovery. Today, 70% of the Brazilian population lives in the BAF region, which has experienced intense urbanization since the 1960s fueled by the rural exodus of people in search of urban jobs. Opposite to what is predicted by the forest transition, this migration coincided with a deforestation wave in the BAF, because subsistence agriculture was replaced by large sugarcane and soybean plantations [38]. Also in contrast to the forest transition prediction, secondary forest patches are becoming increasingly younger due to shortening fallow periods in slash-and-burn agriculture [39], which reduces forest resilience by depleting soil nutrients [40] and facilitating exotic plant species invasions [41]. Instead of experiencing a net gain of forest cover, many agricultural landscapes are experiencing increasing forest degradation, threatening native biodiversity persistence [23,42].

Additionally, forest gains do not necessarily benefit biodiversity persistence if forest species remain exposed to exploitation either for subsistence or commercial purposes [43]. It is well documented that local rural populations depend on forests for fuel wood and other forest products, such as bushmeat [35]. For example, bushmeat trade and subsistence consumption can deplete game populations across large (>2000 ha) patches of old-growth forests in the Amazon region [44]. In the context of HMLs, forest loss and fragmentation usually facilitate hunting, forest exploitation, and forest fires, because they increase forest accessibility, permit regular forest clearing via fire, and induce negative edge effects on forest wildlife [45]. Increasing human disturbance and forest degradation result in severely defaunated landscapes where most medium-to-large vertebrates become regionally extinct or occur at reduced abundances even in protected areas [2,46]. Thus, given the growing demand for agricultural products and current trend of land-use intensification for agriculture, increases in forest cover as well as in vulnerable biodiversity via forest transition are unlikely [47]. Therefore, strategies for biodiversity conservation out of protected areas should move beyond the dichotomy between 'land sparing' and 'wildlife-friendly farming' if we want to generate an integrative approach able to promote both biodiversity conservation and agricultural production [8,48].

The role of secondary forests

Context matters

HMLs typically contain patches of regenerating or secondary forests [49], which globally account for more than 50% of remaining tropical moist forest [50,51]. This figure, plus the assumption of ongoing forest transition, has led scientists to ask whether regeneration or secondary forest patches are able to guarantee long-term biodiversity persistence as regrowth forests expand their coverage across HMLs [52]. Whereas some studies have recorded significant portions of the original biota in secondary forests [53,54], others argue that these areas tend to retain impoverished subsamples of local biotas, with limited potential for conserving species and ecosystem services in the long run [22,28].

Such contrasting perspectives regarding the conservation value of secondary forest patches probably result from differences in context, including biogeographic aspects [55], landscape spatial configuration [24], climate [21], and patterns of human disturbance [56]. Many of the examples of HMLs in which secondary forest patches apparently retain an important fraction of the original biota, come from recently deforested landscapes, such as new agriculture frontiers [57]. Such landscapes share the following traits that are likely to increase the conservation value of the secondary forest patches therein: (i) they are predominantly forested, therefore supporting large, viable wildlife populations as sources for colonizing new secondary forest patches; and (ii) the human population is low, resulting in low levels of exploitation and disturbance in the secondary forest patches. In such a 'biodiversity-friendly' context, secondary forest patches might not only be eventually inhabited by forest-dependent species, but also retain much of the local forest biodiversity.

In highly deforested and disturbed landscapes, the remnant forest patches are unlikely to contain the full suite of mature forest species for colonization of new secondary forest patches. In such landscapes, a few species that thrive at forest edges typically increase in abundance in remnant forest patches, and this is thought to cause cascades of species reductions and extirpations [28]. For example, in Amazonian forest fragments, ecologically plastic and generalist native plant species experience up to a tenfold increase, whereas the old-growth flora becomes increasingly rare [58]. Apparently, such 'winner species' are favored by altered microclimate conditions resulting from structural collapse along the edges of remnant patches [59]. Such changes have led to the idea that forest edges and small forest remnants move toward early-successional systems, a phenomenon termed 'retrogressive succession' [60].

In landscapes where remnant forest patches have reverted to an early-successional state after such a retrogressive succession, forest regeneration on abandoned lands is not expected to bring back patches of late-successional or mature old-growth forests. Rather, these patches will remain in an early- or intermediate-successional state. We expect a critical level of edge-affected habitats, above which forest regeneration and the emergence of late-successional forests are limited [60]. Therefore, depending on the amount of remaining intact mature forest in the landscape, regenerating forests in HMLs can either move towards a highly diverse and structurally complex state, or towards a state of low-to-intermediate levels of biodiversity and structural complexity.

Finally, small-scale disturbances are usually neglected in large-scale studies, but some recent evidence suggests that secondary forests exposed to persistent pressures by edge effects, fuel wood harvesting and hunting can arrest or divert forest succession [61]. Accordingly, the emerging concept of 'novel ecosystems' proposes that human activities, even those of relatively small impact, will dictate the future of disturbed forests, and that we should not assume that they will naturally return to a wild, biodiverse state [49]. Advocating for a crucial conservation role played by secondary forest patches should therefore be viewed with some skepticism [62]. Subsequent to the initial and usually major waves of forest clearing and land abandonment, forests continue to experience small-scale disturbances as long as they remain part of unmanaged HMLs [63].

Disturbance and conservation thresholds

Ecosystem services, such as carbon storage, soil protection, water cycling, and provision of forest products, are positively correlated with forest aboveground biomass [62]. As disturbance proceeds and harvest of forest products intensifies, forest biomass in a landscape will cross a threshold, thus greatly reducing the services and products provided

Box 2. Human disturbance and forest degradation

We hypothesize that there must be a range of disturbance intensity [from low to medium (Figure I, green area)] within which human disturbance is not sufficiently high to trigger irreversible forest degradation (Figure I, red area), enabling altered landscapes to retain a high level of biodiversity. In other words, below a disturbance threshold, forest remains resilient to disturbances and able to retain biodiversity and landscape conservation value. At disturbance and conservation thresholds (Figure II), any additional disturbance will drive the landscape towards a state of degradation (Figure II, red area), which is not expected to revert back to sustainable states (Figure II, green area) unless intense restoration initiatives are applied. Such a degraded landscape is also expected to cross a conservation threshold, reducing its priority level for biodiversity-conservation initiatives (i.e., limited conservation value). Unfortunately, many altered landscapes worldwide are currently moving fast towards a degraded state.

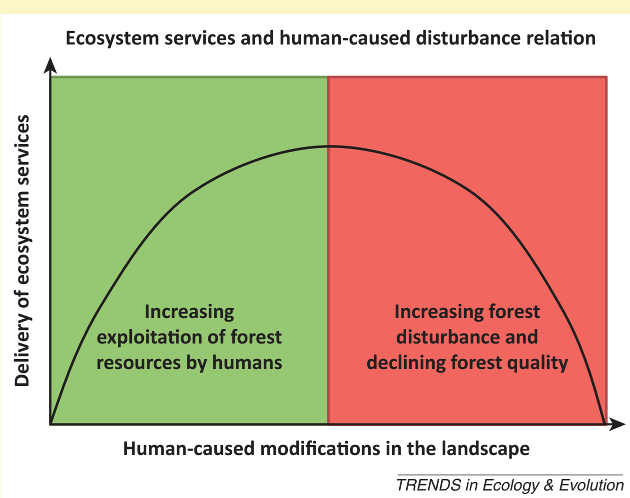

Figure I. Delivery of services depends on the presence of humans to receive them; therefore, up to a point, increasing human population in the landscape increases its provision of services (e.g., fuel wood and hunted wildlife). Beyond that point, human-caused disturbances tend to reduce both the quality of the habitat and provision of ecosystem services. Colors represent sustainable (green) and unsustainable (red) managed landscapes.

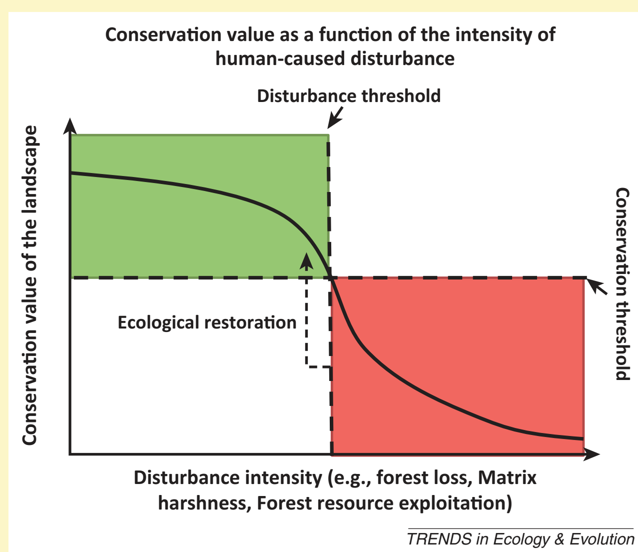

Figure II. Increasing human-caused disturbance reduces the conservation value of sustainable tropical landscapes (green) as well as causing their degeneration into unsustainable states (red) that are likely to have crossed both conservation and disturbance thresholds. Only ecological restoration (arrow) might turn such degraded landscapes into healthy ecosystems.

by that forest [64]. This connection between human disturbance, forest biomass, and provision of ecosystem services implies that a maximum level of services (including forest goods) can be obtained at moderate levels of disturbance at local and landscape scales (see Figure I in Box 2).

However, most tropical forest biotas have already lost more than 70% of their original forest cover, and the remaining cover tends to persist as edge-affected remnants situated within an agricultural matrix that is inhospitable to most forest-dependent species [65,66]. Highly fragmented or edge-dominated landscapes are not expected to offer appropriate habitat for forest-dependent or old-growth forest species [22], but instead will favor disturbance-adapted species that tend to proliferate over large areas, reducing β diversity and generating taxonomic and functional homogenization [23,67]. Therefore, one would conclude that, as long as edge-affected or degraded forests dominate HMLs at the expense of mature forests, the conservation value of such landscapes will remain limited (see Figure II in Box 2).

Multiple pathways for HMLs

Based on the evidence discussed so far, we propose a conceptual model describing potential trajectories for tropical forest landscapes (Figure 1). Initially, deforestation converts ‘natural landscapes’ into ‘conservation landscapes’ (Figure 1; flow 1), which retain a high old-growth: secondary forest ratio and low coverage of edge-affected habitats. Following further forest loss and fragmentation, conservation landscapes move towards ‘functional landscapes’, with intermediate old-growth:secondary forest or old-growth:edge-affected habitat ratios (Figure 1; flow 2). These two categories of HMLs can be considered biodiversity-friendly landscapes because they have high prospects for long-term biodiversity persistence and provision of ecological services.

However, functional landscapes can move through two contrasting trajectories. In the first, if land abandonment occurs and is combined with forest protection, such that large blocks of regenerating forest emerge and move towards late-successional or even old-growth forests, a functional landscape can return to a conservation landscape (Figure 1; flow 3). In the opposite direction, functional (and conservation) landscapes can experience additional demands for land, resulting in further forest loss and increased human disturbance (e.g., logging, hunting, or plant collection). This drives functional or conservation landscapes towards ‘degraded landscapes’ (Figure 1; flows 4 and 5), which tends to comprise small patches of edge-affected forest [68], with low biodiversity and low provisioning of ecosystem services (i.e., limited conservation value). Degraded landscapes can revert back to either functional or conservation landscapes exclusively via active, extensive ecological restoration of abandoned lands and strict forest protection (Figure 1; flow 6).

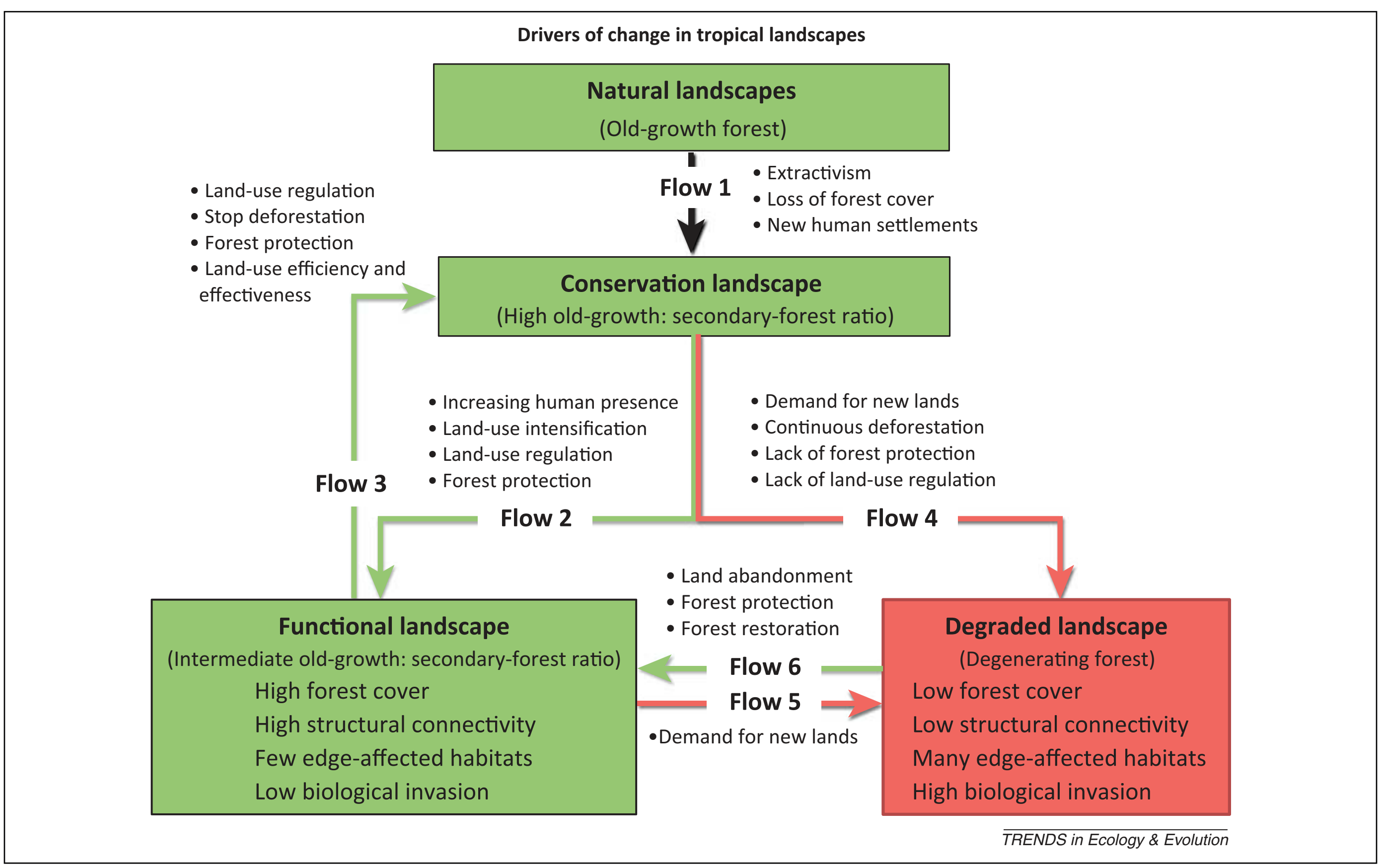

Figure 1. Conceptual model of the possible trajectories of tropical forested landscapes as shifts among three types of sustainable (green) and one type of unsustainable (red) landscape. Each flow denotes a series of linked driving factors indicated in the bulleted list next to each arrow. After the arrival of the agricultural frontier (black arrow), biodiversity-friendly farming (green arrows) can promote food sovereignty, ecosystem services, and biodiversity conservation in human-modified landscapes (HMLs). Intensive land use and natural resource exploitation (red arrows) tend to push HMLs towards unsustainable, degenerate configurations.

The key role of agriculture

One key element that will determine whether these landscapes tend to move towards a sustainable or unsustainable configuration is the dominant type of agriculture. Agriculture will influence the permeability of the nonforested matrix and the likelihood of biodiversity persistence and recovery in HMLs [48]. This is the field where the debate between land-sparing and wildlife-friendly farming flourishes [7]. Although resolving such a dilemma is beyond the aims of this article, we believe that the more that intensive land uses (e.g., pastures and monocultures) dominate these landscapes, the more unsustainable they tend to be (Figure 1; flows 4 and 5). By contrast, as long as biodiversity-friendly farming systems dominate the landscapes (Figure 1; flows 1; 2 and 3) or emerge in response to land abandonment (Figure 1; flow 6), the higher the probability of having sustainable landscape configurations that couple both food sovereignty and biodiversity conservation. In our opinion, both small-scale agriculture and agribusiness have the potential to contribute to either scenario depending on the socioeconomic forces driving such changes, and we recognize both sectors as important players for the dynamics of land-use shifts in the tropics.

Theoretical and applied implications

Although our trajectory model represents a simplification of the real world, it makes at least two important contributions. First, it identifies, classifies, and establishes causal connections between the major forces determining shifts among tropical HMLs. Here, it is important to mention that global climatic change can also affect HML trajectories, because current models of climate change predict a reduction in precipitation in many tropical forests over the next few decades [69]. This could hasten the transition of conservation and functional landscapes to degraded landscapes, and even natural landscapes could change to savanna-like and treeless ecosystems. Second, the model implies that the emergence and persistence of biodiversity-friendly landscapes will not naturally result from patterns of land use regulated exclusively by economic interests, whether commercial or subsistence. Rather, the proliferation and long-term persistence of biodiversity-friendly landscapes depend on land-use regulation and forest protection and management, to ensure the persistence of high-quality forest habitat (large areas of either old-growth or late-successional forests) and a functional configuration of that forest. Conservation biologists, decision makers, and practitioners can address either conservation or development programs and act accordingly. More precisely, increasing effort in terms of research, land-use regulation, conservation planning, and participatory work (among land users, academic, and non-academic stakeholders) is required to achieve win-win balances between biodiversity conservation, provision of ecosystems services, and human well-being across HMLs [53,70]. Therefore, we hope that this article will serve as both a practical and a theoretical framework for the study and management of true biodiversity-friendly landscapes.

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