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Research Article

The Effects of Selective Logging Behaviors on Forest Fragmentation and Recovery

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To study the impacts of selective logging behaviors on a forest landscape, we developed an intermediate-scale spatial model to link cross-scale interactions of timber harvesting, a fine-scale human activity, with coarse-scale landscape impacts. We used the Lotka-Volterra predator-prey model with Holling's functional response II to simulate selective logging, coupled with a cellular automaton model to simulate logger mobility and forest fragmentation. Three logging scenarios were simulated, each varying in timber harvesting preference and logger mobility. We quantified forest resilience by evaluating (1) the spatial patterns of forest fragmentation, (2) the time until the system crossed a threshold into a deforested state, and (3) recovery time. Our simulations showed that logging behaviors involving decisions made about harvesting timber and mobility can lead to different spatial patterns of forest fragmentation. They can, together with forest management practices, significantly delay or accelerate the transition of a forest landscape to a deforested state and its return to a recovered state. Intermediate-scale models emerge as useful tools for understanding cross-scale interactions between human activities and the spatial patterns that are created by anthropogenic land use.

1. Introduction

Humans both create and respond to spatial patterns across a range of spatial and temporal scales [1–3]. Although the real world is multiscale [4, 5], most models of land use and land cover change are built at a single spatio-temporal scale. Social-ecological dynamics tend to be most predictable at broader analytical scales (i.e., broad extent and coarse grain), in part because analysis that uses a higher level of data aggregation obscures the variability of processes (such as idiosyncratic decisions by people) that occur at finer scales [4, 6–8]. Broad-scale models, however, often lack important elements of complex processes that can be modeled using a multi-scale approach [9–11].

Land use is both a response to socioeconomic driving factors (e.g., the price of beef) and a cause of changes in socioeconomic systems (e.g., forest clearing for increased cattle production leads to an increased supply of beef, reducing prices) [12, 13]. Influences on land use occur at many different scales, and their interactions and feedbacks can create nonlinear dynamics and the potential for alternate stable states [14–16]. Cross-scale interactions can have important influences on fine-scale processes, or vice versa [17, 18]. In this context, intermediates or mesoscale models, which focus on connecting fine- and broad-scale pattern-process relationships [19], have an important role to play because they are well suited to capturing human agency, an important element that many models of land-use ignore [8, 10, 20, 21].

We used intermediate-scale models to evaluate the broad-scale impacts of selective logging, a fine-scale process, on a simulated forest landscape. In the Amazon basin, selective logging has great economic importance but is also a large-scale driver of forest fragmentation [22–24]. Although timber loggers do not clear-cut the forest and burn

it for land conversion, they thin the forest by harvesting marketable tree species. In the process they typically degrade the forest, damaging both the canopy and the understory [25–27]. One of the current concerns in the Amazon is that timber harvesting may degrade a forest to the point of passing one or more key thresholds, beyond which the forest can lose its ability (at time scales of >50 years) to both sustain biodiversity and provide important ecosystem goods and services [28–30]. Such changes can be considered a regime shift: a substantial reorganization of a complex system with prolonged or irreversible consequences [31–33].

Thus far, most studies on selective logging have focused on quantifying the extent, distribution, and rate of selective logging in the forest landscape [24, 26, 38]. Such studies have found that selective logging can leave a complex array of canopy gaps caused by tree falls, roads, skid trails and log decks [27, 39, 40]. Selective logging has also been found to cause alterations in forest biophysical properties (e.g., water and wind stress and changes in micro-meteorological systems [41]), which could lead to forest fires [25, 42] and changes in forest structure and composition [43]. Although these studies are important, they have not linked the direct effects of different logging approaches to their coarse-scale landscape impacts.

The purpose of this study was to determine whether different selective logging behaviors could influence the resilience of a simulated forest landscape. We constructed three scenarios, representative of logging behaviors in the Peruvian Amazon [44]. In scenario 1, we simulated a null model, where selective logging occurred randomly and there was no timber harvesting preference. In scenario 2, we simulated the behavior of timber loggers that harvest valuable timber species at a high mobility cost [44]. In scenario 3, we simulated the behavior of loggers that harvest timber species of low value at a low mobility cost, because species of high value have already been harvested [44]. Note that the focus of this analysis was on the spatial patterns of impacts, rather than on logging intensity. For each scenario, we quantified forest resilience by evaluating: (1) spatial patterns of forest fragmentation and the transition time to reaching a deforested state; and (2) the time taken to return to a forested state through management. We defined social-ecological regime shifts as being the transitions between (1) an old-growth forest state (timber is abundant) and a deforested state (entire forest landscape has been logged); (2) a deforested state and a recovered (forested, but not old growth) state [45]. In the recovered state, timber trees reach a minimum commercial volume in the short term and in the long term, more complete ecological function may return. In both cases, the states under consideration are social-ecological rather than purely ecological states; the stability or instability of patterns on the landscape is contingent on human agency and decisions as well as on the ecology of the system.

2. Methods

We developed an intermediate-scale approach to model timber and logger dynamics. Published data were used to parameterize the model when they were available (Table 1). The model consisted of three main parts: (1) a module with timber density, volume and distribution; (2) a module simulating logger-timber dynamics, (3) a cellular automaton module simulating logger mobility and fragmentation. The simulated forest landscape consisted of a two-dimensional space of 65 × 65 1-ha cells (4225 cells or ha), the area of a small forest concession in southwestern Amazonia [44]. Following Peters et al. [19], our modeling approach incorporated three scales. The finest scale (single cell = 1 ha) was the scale at which individual timber trees were found, selective timber logging occurred, and logged forest patches began forming. Key pattern-process relationships at this scale included timber harvesting that influence the distribution and abundance of timber trees in the landscape. The intermediate-scale (>1 cell or 1 ha) was the scale at which loggers dispersed to other forest cells and the number of logged forest patches increased. Key pattern-process relationships at this scale included the spatial patterns of loggers and their mobility processes. The coarse scale is the scale at which forest fragmentation occurs. Key pattern-process relationships at this scale consisted of the spatial patterns of logged forest patches and the transition to the forest degradation state, in which the provision of timber was exhausted.

2.1. Timber Density, Volume, and Distribution. In southwestern Amazonia, the density of timber species of low and high value can show considerable variation. Highly valuable timber species as mahogany (*Swietenia macrophylla*) can have densities >0.03 trees ha^{-1} [36], whereas the density of Spanish cedar (*Cedrela odorata*) can range from 0.17 to 0.35 trees ha^{-1} [46]. Timber species of much lower value as *Cedrelinga catenaeformis* can be found at much higher densities (e.g., 0.8 trees ha^{-1} [46]). Furthermore, logging intensity in this region varies from 1 to 6 trees ha^{-1} [47].

We assumed that the forested landscape consisted of an old-growth forest, where timber trees of high and low value coexisted, regardless of species. The density of timber trees of high value in the simulated landscape was set at 0.5 trees ha^{-1}, which is within the range (0.3 to 2 tree ha^{-1}) found in Verissimo et al. [48]. In the Peruvian Amazon, the minimum cutting diameter (MCD) of trees of high value such as mahogany is ≥75 cm dbh or ≥ 4.5 m^3 per tree ("real volume"), but they can also reach volumes as high as 21–27 m^3 (150–190 cm dbh) [36, 49]. We set the volume of timber trees of high value to range from 5 to 26 m^3. Thus, the volume density for timber trees of high value in the simulated forest landscape ranged from 2.5 to 13 m^3 ha^{-1}, which is similar to the range of mahogany volumes (1−11 m^3 ha^{-1}) found in Verissimo et al. [48]. The density of timber trees of low value was set at 4 trees ha^{-1}, within the range of the extraction rate in southwestern Amazonia [47]. The volume of timber trees of low value ranged from 12 to 47 m^3 ha^{-1}; this is equivalent to 3–12 m^3 per tree [37]. The volumes of both types of timber trees were drawn randomly from a normal distribution and were placed randomly within the cells of the forest landscape at the start of each simulation.

Table 1: Summary of parameters for the Lotka-Volterra component of the model.

Parameter	High-value tree	Low-value tree	Citation
r, intrinsic growth rate for trees (timber volume)	$0.02\,\mathrm{m}^3\,\mathrm{yr}^{-1}$	$0.04\,\mathrm{m}^3\,\mathrm{yr}^{-1}$	[34, 35]
a, harvesting volume per time step (harvesting rate)	$8\,\mathrm{m}^3$	$4\,\mathrm{m}^3$	[36, 37]
b, conversion efficiency	20%	20%	
d, declining rate of logger population in absence of local timber	2%	2%	
c, maximum harvesting rate	$20\,\mathrm{m}^3\,\mathrm{ha}^{-1}$	$40\,\mathrm{m}^3\,\mathrm{ha}^{-1}$	[25]
K, carrying capacity (maximum volume) for a timber tree	$28\,\mathrm{m}^3$	$12.5\,\mathrm{m}^3\,\mathrm{yr}^{-1}$	[36, 37]

2.2. Timber-Logger Dynamics Module. We used an adaptation of the Lotka-Volterra predator-prey equations [50, 51] to simulate the harvesting of timber resources (N_1) by a mobile predator, the logger (N_2). Timber volume growth was modeled using the logistic growth function with Holling's functional response II; that is, the timber harvesting rate (predation attack rate) increased in a decelerating fashion, reaching a maximum harvesting rate (c) at high timber volumes. The Lotka-Volterra equations are:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{rN_1(K-N_1)}{K - c(1-1/e^{aN_1/c})N_2} \quad \text{timber,} \\ \frac{dN_2}{dt} &= \mathrm{bc}\left(1 - 1/e^{aN_1/c}\right)N_2 - dN_2 \quad \text{logger,} \end{aligned} \tag{1}$$

where r is the intrinsic growth rate for timber volume growth, a is the harvesting rate, b is the conversion efficiency, d is the declining rate for loggers, c is the maximum harvesting rate, and K is the carrying capacity for a timber tree.

Equation (1) were modified to introduce one logger and timber trees of low and high value. Situations with one predator and two prey items typically use a competition coefficient for prey 1 on prey 2 (α_{12}) and for prey 2 on prey 1 (α_{21}). However, we assumed that there was no competition between timber trees of low and high value, and hence competition coefficients (α_{12} and α_{21}) were equal to zero. The modified Lotka-Volterra equations were thus:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{r_1N_1(K_1-N_1)}{K_1} - c_1\left(1 - \frac{1}{e^{a_1N_1/c_1}}\right)N_3 \\ &\qquad \text{low-value timber trees,} \\ \frac{dN_2}{dt} &= \frac{r_2N_2(K_2-N_2)}{K_2} - c_2\left(1 - \frac{1}{e^{a_2N_2/c_2}}\right)N_3 \\ &\qquad \text{high-value timber trees,} \\ \frac{dN_3}{dt} &= bc_1\left(1 - \frac{1}{e^{a_1N_1/c_1}}\right)N_3 + bc_3\left(1 - \frac{1}{e^{a_2N_2/c_2}}\right)N_3 - dN_3 \\ &\qquad \text{logger.} \end{aligned} \tag{2}$$

We obtained parameter values from the literature, making some assumptions (as explained below) due to lack of data. A mean tree growth rate of $0.03\,\mathrm{m}^3\,\mathrm{yr}^{-1}$ has been reported for mahogany trees [34]. We took a lower volume growth rate because tree growth is typically non-linear, having low growth rates for small and large-sized individuals and high growth rates for the intermediate sizes (e.g., [35, 52]). We set the growth rates of timber trees of high value (r_2) at $0.02\,\mathrm{m}^3\,\mathrm{yr}^{-1}$ and the average growth rate for timber trees of low value was set at $0.01\,\mathrm{m}^3\,\mathrm{yr}^{-1}$ for a total value of (r_1) $0.04\,\mathrm{m}^3\,\mathrm{yr}^{-1}$. Carrying capacity was defined as the maximum volume that timber of low and high value can be achieved in an old-growth forest. The carrying capacity for a timber tree of high value (K_2) was set at $28\,\mathrm{m}^3$, the maximum real volume for mahogany trees in an old-growth forest [36], and that of low value was reached at about $12.5\,\mathrm{m}^3$ [37] for a maximum volume (K_1) of about $50\,\mathrm{m}^3$ for 4 trees.

Where timber trees of both low and high value were found, the minimum commercial harvesting volumes for each were set $8\,\mathrm{m}^3$ (a_1) and $4\,\mathrm{m}^3$ (a_2). These volumes were equivalent to harvesting low-and high-value timber trees above their MCD [36, 37]. In terms of low-value timber trees, the harvesting of $8\,\mathrm{m}^3$ could be compared to harvesting 2 trees of *Cedrelinga catenaeformis*, each one ≥61 cm dbh (MCD) [37]. Timber trees were only harvested when they were greater than or equal to their minimum harvesting or commercial volume. Due to previous logging, some forest concessions in southwestern Amazonia have very low numbers of high value timber species; thus, timber loggers in these concessions have a preference for harvesting timber species of low value at very high rates [44]. The maximum harvesting rate for timber trees of low value (c_1) was set at $40\,\mathrm{m}^3\,\mathrm{ha}^{-1}$ and for high value was set at $20\,\mathrm{m}^3\,\mathrm{ha}^{-1}$ (c_2), a low intensity extraction [25]. Each logging team consisted of 3 loggers [53]. A 20% conversion efficiency (b_1 and b_2) was assumed to be associated with harvesting timber and logger population growth. If there was no timber to harvest, we assumed that the population of loggers declined (d_1 and d_2) by 2% per year.

2.3. Cellular Automaton Module. We coupled the Lotka-Volterra predator-prey model with a cellular automaton model [54, 55]. In this study we assumed that timber logging was associated with the opening of the forest canopy. Each forest cell contained timber trees of either low or high value and in some cases both types. Before logging, all forest cells in the landscape were in the unlogged state (cells = 1) and they transitioned into the logged state (cell = 0) when timber from a cell was harvested. The cell remained in the logged state for the duration of the simulation ($t = 80$ years), although timber volume kept on growing. A logger dispersed into a new forest cell when timber volume was $< a_1$ or a_2, the threshold

volume. A logger could return to a previously logged cell if there was timber Larger than or equal to threshold volume. The simulation model started with 89 teams of three loggers per cell, placed in the forest cells closest to a hypothetical road in the forest landscape. We do not know the actual number of loggers that work in the forest concessions in southwestern Amazonia, but experienced foresters who work in the region indicate that after the first forest concession contract of 40 years, most of the high value timber species are depleted, particularly in the Tambopata and Manu regions of Madre de Dios, Peru [pers. comm. Cossío 2010]. In our simulations this situation occurred when there were about 89 teams of loggers.

2.4. Selective Logging Scenarios and Data Analysis. We contrasted three different scenarios to explore the long-term effects of different selective logging behaviors on forest fragmentation (Figure 1(a)). The differential equations used for are presented in the Appendix. All modeling was done using MATLAB 7.6. In *scenario 1*, logger mobility was random within the forest landscape and there was no timber harvesting preference. Loggers had a 50% chance of harvesting timber trees of either low or high value when both types of timber were present in a forest cell (Figure 1(a)). This scenario was used as a null model for comparison purposes, since we simulated an expected behavior in the absence of any specific processes [56, 57].

In scenarios 2 and 3, loggers had a timber harvesting preference and were assumed to access timber sequentially, along an accessibility gradient, starting from a hypothetical road and using a mobility cost function. In both scenarios, loggers preferred to disperse to forest cells closer to the road to reduce transportation costs. In *scenario 2*, loggers harvested timber trees of high value and when both timber trees were present there was a 75% chance of harvesting timber of high value (Figure 1(a)). In this scenario, a mobility cost was introduced using linear relation between distance to the road (line-haul cost) and transport cost [58]. Scenario 2 simulated the behavior of timber loggers in forest concessions that harvest highly valuable timber species such as mahogany and Spanish cedar and depend heavily on roads for timber transport [44]. In *scenario 3*, loggers harvested timber trees of low value and when both timber trees were present there was a 75% chance of harvesting timber of low value (Figure 1(a)). The mobility cost in this scenario was based on a logistic function between distance to the road and transportation cost. Scenario 3 simulated the behavior of timber loggers in forest concessions that harvest timber species of low value and have much less financial capital to invest in road construction [44]. These loggers tend to use a combination of roads and rivers to reduce transport costs [44].

To estimate the time until a regime shift to forest degradation occurred, each simulation model was run for 80 years for a total of 50 times. By this time the entire forest landscape was logged and very little timber was left. In scenario 2, the harvesting of high-value timber trees ended 36 years after the initiation of logging; thus, for the remaining time of the simulations we assumed that loggers

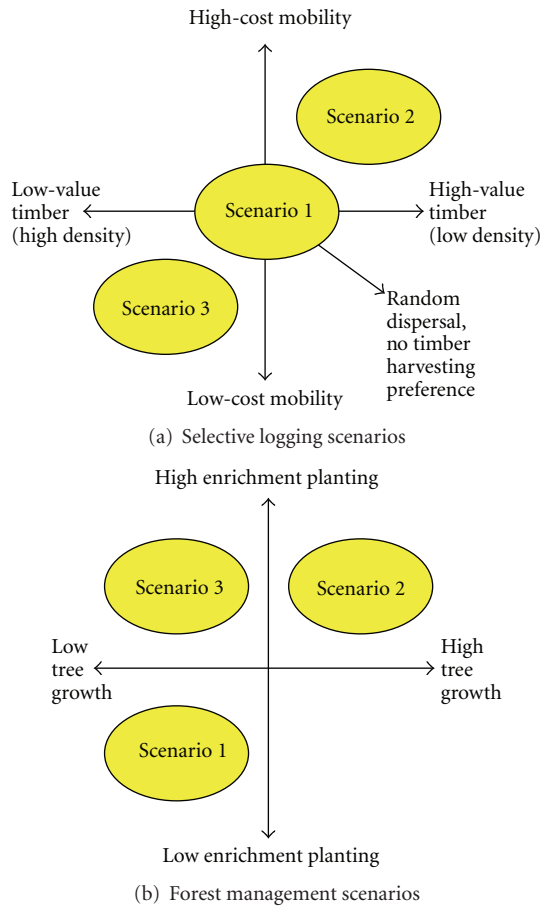

Figure 1: Three selective logging scenarios, based on timber harvesting preference, mobility cost, and forest management practices, were simulated in a forest landscape.

changed their harvesting preference to timber trees of low value, which is very common [44]. We analyzed the spatial patterns of forest fragmentation for each scenario at the scale of the concession landscape (4225 cells or has). Landscape pattern metrics were calculated in Fragstats 3.3.1 using the 8-neighbor-cell rule [59]. We quantified the number of logged forest patches, length of edge, and area logged in the concession landscape for each year of simulated selective timber logging.

2.5. Forest Management Scenarios and Data Analysis. Once the forest landscape was in the deforested state, we explored the transition of the forest landscape to a recovered state by associating logging behaviors with different forest management practices (Figure 1(b)). We estimated the time of reaching a recovered state, defined as the system recovery after a perturbation where timber in the forest cells grew to a minimum commercial volume. The recovered state was assumed to be an alternative state [45] because these forests are assumed to be actively managed for the long-term production of timber and often exhibit a different floristic composition and structure from the prelogged state. Due to

the low timber yields at the end of 80 years of logging simulation (<0.1 m^3/ha), we enhanced timber recruitment by assuming the use of enrichment planting of timber saplings during harvesting. In all scenarios we used higher tree growth rates to simulate silvicultural thinning and exposure to high light intensities due to canopy opening from logging.

In *scenario 1*, we simulated the lowest levels of forest management practices (Figure 1(b)). We assumed that timber trees of high value could reach a volume ranging of 0.5-1 m^3 at the end of logging simulations, equivalent to mahogany trees of ∼30–40 cm dbh [36]. We assumed that timber trees of low value could reach a volume ranging 1.5–2 m^3, the equivalent to two trees per cell >30 cm dbh. This was calculated with a diameter-volume equation for trees of low commercial value (Vol = 9.1405 $\text{dbh}^{2.1382}$, r^2 = 0.95, n = 38), using the data from Lombardi et al. [37]. In this scenario timber growth rates were set for r_1 and r_2 at 0.03 and 0.06 $m^3\,yr^{-1}$ [34]. In *scenario 2*, we assumed that there were higher levels of forest management practices (Figure 1(b)). We assumed that timber trees of high and low value could reach 1–1.5 m^3 (a mahogany tree of 40–60 cm dbh [36]) and 2–2.5 m^3 (corresponding to two timber trees of low value >35 cm dbh using the equation above). Timber growth rates for low (r_1) and high (r_2) value timber were 0.04 and 0.08 $m^3\,yr^{-1}$ [34]. In *scenario 3*, there were intermediate levels of forest management practices. Enrichment planting levels were as high as the values in scenario 2, but timber growth rates were as low as the values in scenario 1 (Figure 1(b)).

3. Results

The amount of timber harvested in each selective logging scenario varied through time. Selective logging under scenarios 1 and 2 harvested the lowest amount of timber, about 0.80 $m^3\,ha^{-1}$ and 1 $m^3\,ha^{-1}$, respectively (Figure 2). Selective logging under scenario 3 harvested the highest amount of timber, reaching rates >35 $m^3\,ha^{-1}$. Out of the three scenarios, scenario 2 harvested the lowest amount of timber (0.40 $m^3\,ha^{-1}$) at the initiation of logging (Figure 2). In this scenario there was a harvesting preference for timber trees of high value, which were exhausted when about 50% of the landscape had been logged. Once the high-value timber trees were exhausted (below commercial volumes), loggers switched their harvesting preference to timber trees of low value, harvesting them at much higher rates.

The three selective logging behaviors or scenarios created different spatial patterns of forest fragmentation. In all three logging scenarios, the number of logged forest patches varied nonlinearly through time (Figure 3). Scenarios 1 and 2 created unimodal trajectories in the number of logged forest patches, whereas scenario 3 created a slightly bimodal trajectory (Figure 3). Throughout the simulations, scenario 2 produced the lowest number of logged forest patches (<50 logged forest patches), but their sizes were much greater than those of scenarios 1 and 3 (Figure 3). The number of logged forest patches in scenario 2 peaked when about 50–60% of the forest landscape (4225 ha) had been logged, ∼30 to 40 years after the initiation of timber harvesting (Figure 3). Scenarios 1 and 3 produced >300 and >250 logged forest patches and their numbers peaked when about 20% of the forest landscape had been logged, ∼10 to 11 years after the initiation of timber harvesting (Figure 3).

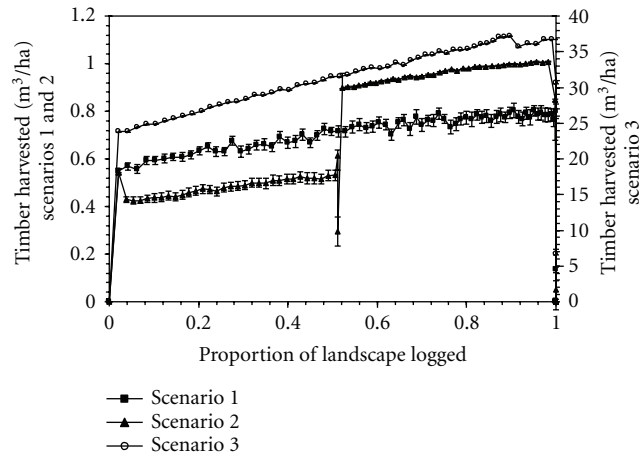

Figure 2: Timber harvested rates over 80 years of selective logging simulations.

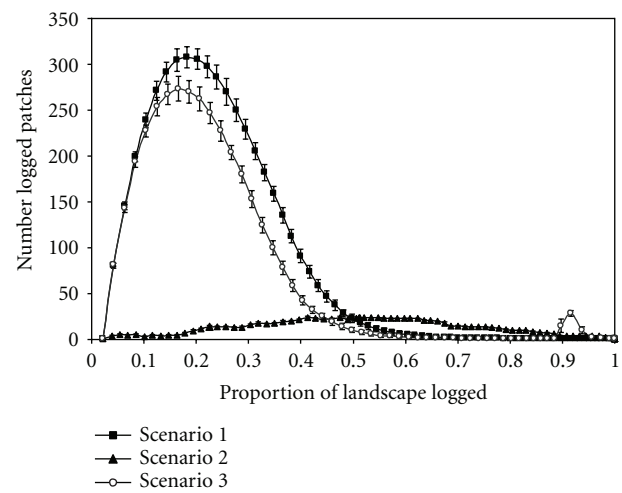

Figure 3: Number of logged forest patches over 80 years of selective logging simulations in a forest landscape (4225 ha).

The three logging scenarios also produced non-linear edge-length trajectories of quadratic form (Figure 4). Scenarios 1 and 2 produced unimodal edge-length trajectories, whereas scenario 3 produced a slightly bimodal trajectory. During the simulations, scenarios 1 and 2 produced the highest edge-length peak at about 400 km, when about 50% of the landscape had been logged, ∼28 and 33 years after the initiation of logging. Scenario 3 produced the lowest edge-length peak at about 350 km, when >40% of the landscape had been logged, ∼23 years after the initiation of logging.

The three selective logging behaviors also delayed or accelerated the transition of the forest landscape to a deforested state. Both scenarios 1 and 2 took >66 years to transition to the deforested state, but scenario 3 transitioned

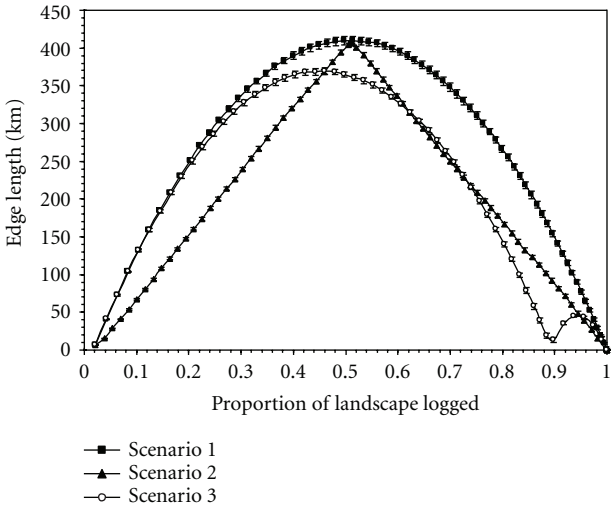

Figure 4: Edge length over 80 years of selective logging simulations in a forest landscape (4225 ha).

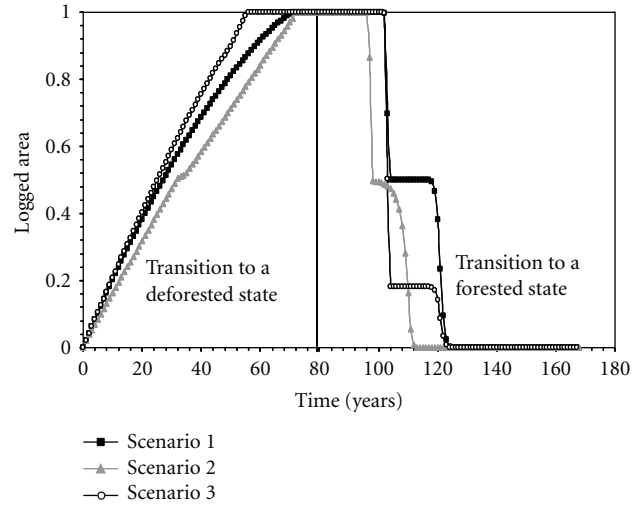

Figure 5: Regime shifts into a deforested state and recovered state in a forest landscape, under three different scenarios of selective logging and forest management practices.

10 years earlier (>51 years) (Figure 5). Forest management practices also delayed or accelerated the transition to a recovered state (Figure 5). When higher levels of enrichment planting and more intensive silvicultural thinning practices were used (e.g., higher timber growth rates), scenario 2 reached the restoration state ∼32 years after entering the deforested state, but when lower levels of these factors were used, scenarios 1 and 3 took a longer time to reach the recovered state (>32 years) (Figure 5).

4. Discussion

Selective timber logging is not often considered as a source of forest fragmentation; however, depending on the harvesting intensity, logging operations can greatly reduce canopy cover (up to 60% [39]), resulting in extensive forest fragmentation and edge effects. When selective logging takes place, the transition from a forest to a logged forest is not as abrupt as that of forest to land uses such as pastures or agricultural areas. Logging disturbances also create edges. The difference is that logging disturbances adjoining forested areas create soft edges whereas deforested or clear-cut areas adjoining forested areas create hard edges [24]. Soft edges can eventually recover in time through regrowth, reducing their overall influence because the transition becomes less severe [60], but soft edges can transition to hard edges if the logged patch is clear-cut.

Selective logging behaviors can create different spatial patterns of forest fragmentation. Several studies have found that timber harvesting regimes or behaviors can influence the patterns of forest fragmentation in a landscape [61]. In this study, scenario 2, the selective logging behavior associated with harvesting timber trees of high value at a high mobility cost, led to the harvesting of lower timber volumes and the creation of a lower number of logged forest patches in the landscape. Scenario 3, the selective logging behavior involving harvesting timber trees of low value at a low mobility cost, led to the harvesting of high timber volumes and to the creation of a higher number of logged forest patches. As in other studies, the three selective logging scenarios showed non-linear forest fragmentation and edge-length trajectories [57, 61–63]. Scenario 3 showed slightly bimodal fragmentation and edge-length trajectories due to the crossing of a distance threshold of the logistic function of distance to mobility cost. This allowed dispersal into more distant areas for the same mobility cost, increasing the number of logged forest patches and edge length (Figures 3 and 4)

Selective logging behaviors can have different impacts on forest resilience. Other studies have found that selective logging behaviors have highly variable impacts on forests, depending on the use of conventional logging versus reduced impact logging techniques [64–66]. In this study we found that logging behavior can affect the speed of the fragmentation process, accelerating or delaying the transition into a deforested state. Any additional logging after reaching the peak level of fragmentation increased the size of the logged forest patches until they coalesced and declined in number to the point that the entire landscape became one logged forest patch (Figures 3 and 5). In the Amazon basin, harvesting timber species of high value (e.g., mahogany) may have a smaller impact on forest structure and function than harvesting timber species of low value, which are more abundant and are extracted at much higher volumes [48]. Sawmills in the Amazon are involved in the processing of more then 100 tree species [67, 68] and the volume of timber species of high value makes up only a small percentage of the total production (e.g., mahogany is 5% of the total timber production) [48].

We associated the harvesting of timber trees of high value at a high mobility cost (scenario 2) with intensive forest management practices. Harvesting timber of high value is usually associated with timber enterprises that have a high

financial capital to invest in infrastructure (e.g., roads, feeder roads, etc.) and machinery, and a high human capital (e.g., education in forestry, experience in logging, skills and knowledge) to implement forest management plans [44, 48, 68].

Lotka-Volterra predator-prey equations represent one of the simplest dynamic consumer-resource systems [69]. Although real consumer-resource systems are more complex, these equations have been previously used for modeling renewable resources and population dynamics, with man as a predator and the resource base as the prey [70–74]. The main assumption in these studies is that consumer or logger dynamics, as in the case of this study, depend solely on a particular resource. However, it is well known that agents of resource use in the Amazon pursue a diverse portfolio of subsistence and market-oriented activities (e.g., hunting, harvesting of NTFP, shifting cultivation, agroforestry, cattle ranching, and agriculture) in order to spread their risks in an extremely variable environment [75, 76].

This framework to connect cross-scale interactions through the transfer of processes at intermediate scales has been used to study several systems, but not in the analyses of forest fragmentation and degradation by human agents [77–80, among others]. We used logger mobility as the transfer process for linking fine-scale processes with coarse-scale pattern as well as the propagation of selective logging in the simulated landscape. To make our model more realistic, we introduced decision making in loggers based on timber harvesting preference (timber of low value versus high value) and logger mobility (high cost versus low cost) from a hypothetical road. However, logging behavior is more complex and depends on other factors such as timber prices, land tenure, forest policy, and accessibility to local markets, among other factors [81, 82]. To evaluate whether different spatial patterns of forest fragmentation could arise when making simple decisions, we also had to ignore the potential effects of other drivers of landscape change such as forest fires, road network expansion, and land conversion after selective logging [25, 81, 83]. We also assumed that there was no tree mortality, tree competition or further tree recruitment during the tree growth simulations.

Despite some of the obvious limitations of the model, our analysis demonstrates that intermediate-scale models can serve as a useful tool for understanding cross-scale interactions between human activities and impacts to the landscape. Although the drivers of tropical deforestation are very well studied, far less is known about the spatial patterns of forest fragmentation and degradation that agents of different land-use systems in the Amazon create [81, 84]. We focused on selective logging behaviors, but intermediate-scale models could be used to study other land-use agents, their interaction and impacts to the landscape. Such studies can offer some insights into the mechanisms that give rise to the patterns of forest fragmentation found in the Amazon. These models can also contribute to the designing of more sustainable developmental or forestry policies, through their assessment of potential consequences or coarse-scale impacts to the landscape. As we seek to balance societal benefits with the cost of ecological degradation, intermediate-scale models have a potential role in generating perspectives on the causes and consequences of fine-scale actions of agents involved in land use, forest management and policy.

Appendix

We developed the following differential equations based on the harvesting preference.

(a) Logger prefers to harvest timber of low value. This case occurred when timber of low value (N_1) was ≥ threshold volume and it was either the only species present in a cell or timber of high value (N_2) < threshold volume. If present N_2 (<threshold volume) experienced logistic growth and the growth of the logger (N_3) was a function of low quality timber species:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{r_1 N_1 (k_1 - N_1)}{k_1} - c_1\left(1 - e^{-a_1 N_1/c_1}\right) N_3 \quad \text{timber of low value,} \\ \frac{dN_2}{dt} &= \frac{r_2 N_2 (k_2 - N_2)}{k_2} \quad \text{timber of high value,} \\ \frac{dP}{dt} &= b c_1\left(1 - e^{-a_1 N_1/c_1}\right) N_3 - d N_3 \quad \text{logger.} \end{aligned} \tag{A.1}$$

(b) Logger prefers to harvest timber of high value. This case occurred when timber of high value (N_2) was ≥ its threshold volume and it was either the only species present in a cell or timber of low value (N_1) < threshold volume. If N_1 was present, it experienced logistic growth and the growth of the logger (N_3) was a function of high-value timber:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{r_1 N_1 (k_1 - N_1)}{k_1} \quad \text{timber of low value,} \\ \frac{dN_2}{dt} &= \frac{r_2 N_2 (K_2 - N_2 - \alpha_{21} N_1)}{K_2} - c_2\left(1 - e^{-a_2 N_2/c_2}\right) N_3 \quad \text{timber of high value,} \\ \frac{dN_3}{dt} &= b c_2\left(1 - e^{-a_2 N_2/c_2}\right) N_3 - d N_3 \quad \text{logger.} \end{aligned} \tag{A.2}$$

(c) Loggers (N_3) "declined" because there was no timber of either high or low value above their respective threshold volume:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{r_1 N_1 (k_1 - N_1)}{k_1} \quad \text{timber of low value,} \\ \frac{dN_2}{dt} &= \frac{r_2 N_2 (k_2 - N_2)}{k_2} \quad \text{timber of high value,} \\ \frac{dP}{dt} &= -d N_3 \quad \text{logger.} \end{aligned} \tag{A.3}$$

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