

# Modelling weed and vine disturbance in tropical forests after selective logging and clearcutting

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## ABSTRACT

Although tropical rainforests preserve high levels of biodiversity, they are among the most threatened ecosystems globally due to large-scale fragmentation as a result of anthropogenic activities. Overall, fast human-driven habitat destruction is suspected to be one of the major causes of species extinction. The mosaic of vegetation types, which contributes to the incredible diversity of the tropics is highly impacted by large-scale fragmentation. The main causes of such habitat fragmentation are selective logging for valuable timber and agricultural clearance. The knowledge of the short and long-term effects of removing selected species in the tropical rainforests are scarce and need to be further investigated. Some studies about the effects of tropical forest disturbance in the short term have been conducted, but in the long term, there is limited knowledge. In this paper, I consider a system of coupled ordinary differential equations (ODEs) that modelled the dynamics of tropical rainforest subject to selective logging to understand how and why weeds and vine displace and limit tree species. From the empirical data collected on canopy height and plant diversity and the model proposed, I have the evidence of a decreasing tree diversity in tropical forests subject to management in comparison with the same but untouched forests.

## 1. Introduction

Tropical forests provide crucial ecosystem goods and services, such as sequestering carbon from the atmosphere, protecting watersheds and conserving biodiversity (Valentini et al., 2014; Cazzolla Gatti, 2016a,b; Avitabile et al., 2016). Around 40%–75% of all biotic species are indigenous to rainforests, half of all the living animal and plant species on the planet live there and about two-thirds of all flowering plants can be found in rainforests. Tropical forests are among the most threatened ecosystems by large-scale fragmentation due to human activity such as heavy logging and agricultural clearance (Cazzolla Gatti et al., 2015). Actually, the area covered by rainforests around the world is rapidly shrinking. Most prior studies into the impacts of land use in tropical ecosystems on the global carbon cycle and conservation of biological diversity have focused on deforestation (Thompson et al., 2009).

In several countries, forest resource extraction has experienced a shift from clearcutting to selective logging (De Wasseige and Defourny, 2004; Gascon et al., 1998; Drigo et al., 2009; Cazzolla Gatti et al., 2015; Vaglio Laurin et al., 2016). In some regions of the World such as Africa, "selective logging" is of great importance because it allows maintaining a significant forest cover and understock of living biomass. Selective logging (i.e. the practice of cutting down one or two largest trees while leaving the rest intact) is increasingly embraced as an approach which

protects the integrity of forest ecosystems while allowing an appropriate use of resources. This is a concept specifically designed to reconcile the different interests in forests, including the maintenance of biodiversity (Rametsteiner and Simula, 2003; Imai et al., 2012). However, several studies in tropical forests subject to selective logging have shown changes in species composition (Silva et al., 1995; Magnusson et al., 1999; Luna et al., 1999; Ganzhorn et al., 1990), genetic diversity (Jennings et al., 2001), forest structure (Hall et al., 2003; Okuda et al., 2003) and nutrient cycling (Herbohn and Congdon, 1993).

However, the knowledge on the short and long-term effects of removing selected species are scarce and need to be further investigated.

One of the main effects of selective logging on forest dynamics seems to be the local disturbance which involves the invasion of open space by weed, vines and climbers at the expense of the late-successional state cenosis (Schnitzer et al., 2000). In secondary forests (regrowth of clearcut areas), instead, the secondary succession does not significantly involve vines and weeds, being directed by the pioneer tree species towards a climax. There is some evidence that tropical forests subject to selective logging have suffered a decline of biodiversity, both of animals and plants species (Gascon et al., 1998; Thompson et al., 2009; Asner et al., 2005; Imai et al., 2012; Cazzolla Gatti et al., 2015).

Weeds, vines and climbing forest species exhibit a well-known range

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of ecological roles (Darwin, 1867) and are fundamental components in forest dynamics with respect to natural disturbance regimes, from pioneer phase to mature phase, and they regenerate from a range of sources, including dormant seeds, seed rain, pre-established juveniles, and resprouts from damaged adults (Gentry, 1991). Most weeds, vines and climbers are uncommon in old-growth forest ecosystems.

Disturbance plays a critical role in weed invasions in rainforests because it creates opportunities for weeds to claim previously utilised space and resources. Rainforest weeds rarely tolerate shade, so some kind of minor disturbance resulting in an opening of the canopy is usually necessary for weed establishment. Typically, fragmentation and selective logging open up gaps of light in which weeds displace or suppress native species. Otherwise, in natural gaps (e.g. due to big broken branch or standing dead trees) the light space created is usually smaller than in logging gaps and tree saplings seem to be prepared to grow fast to fill the canopy opening (Bais et al., 2003; Perry et al., 2005; Thorpe et al., 2009; Dudley and File, 2007; Callaway and Mahall, 2007). This reduces the likelihood of vines, weeds and climber invasion (Asner et al., 2004; Cannon et al., 1994).

In this work, I will derive a simple model to describe the dynamics of tropical rainforest subject to selective logging. For this purpose, I developed a quantitative, deterministic model that describes the dynamic of tropical trees coexisting with weeds, vines and climbers. I argue that the selective removal of tallest tropical trees creates gaps of light in which weeds, vines and climbers can grow to suppress the sprouting trees. This hypothesis is supported by a dataset of tree heights and weed/vine cover that I collected from 21 plots located in Central and West Africa both in untouched and managed areas. To my knowledge, this is the first mathematical model that builds on those experimental findings to quantitatively explain the presence of weed and vines in forest subject to selective logging. The model is embodied with two simple ordinary differential equations and does not explicitly describe the spatial structure of the forest. My results show that different regime shifts may occur depending on the type of forest management adopted.

## 2. Materials and methods

This work is based on the concept of the vertical structure of the forest (Cazzolla Gatti et al., 2017b). I refer to “structure” as the vertical composition and stratification of vegetational layers, from the understory to the highest trees. In this sense, the vertical structure of a forest may be described by some statistical parameters of height distribution of the trees, like the mean, the standard deviation or a specific percentile. I consider that a forest is well structured when the distribution of trees heights is wide and heterogeneous (Fig. 1). Vice versa I consider forest as unstructured when the distribution of the trees heights is concentrated into a small range and the variability is quite low. For the purpose of this work, I introduce a vertical vegetational structure index ( $h$ ) ranging from 1, the maximum value corresponding to a proxy of a well-conserved old-growth tropical forest, to 0, the minimum value corresponding to a proxy of a highly damaged forest (e.g. clearcut). Intermediate values of  $h$  should indicate that the forest has decreased its height of some amount, but the largest contribution to the index must be given by the tall trees. Therefore, a herd of elephants cutting a path below the (untouched) high canopy, should decrease by little or no amount the value of  $h$ , while the selective logging of commercially-valuable trees, which are the tallest in the forest, should decrease  $h$  by a sizable amount. Such Index may represent a single statistical parameter (e.g. mean canopy height or the standard deviation) as well as an indicator of the combination of more parameters. In this study, because I am interested in the effects on the long-term of the selective removal of higher trees, I assign to the vertical structure index ( $h$ ) the mean of trees height over the 80° percentile. Nevertheless, other statistical parameters will be compared and some discussion will be carried out.

### 2.1. The model

The model includes two state variables: the forest vertical index ( $h$ ), based on the height distribution of the trees over the 80° percentile, and the weeds, vines and climbers cover ( $q$ ). In the absence of any other disturbance, when empty space becomes colonized by a forest, I shall assume that the index  $h$  is subject to the following simple dynamics:

$$\frac{dh}{dt} = r(h)h \quad (1)$$

where the growth rate  $r$  is a decreasing, continuous function of  $h$ , it reaches a positive maximum for  $h = 0$  and becomes zero at  $h = h_{max}$ . It is convenient to rescale all the quantities by using  $[r(0)]^{-1}$  as the unit of time and  $h_{max}$  as the unit of  $h$ . Therefore, the above assumptions on  $r$  can be summarized as:  $r(0) = 1$ ;  $r(1) = 0$ ;  $r'(h) < 0$ .

Because weeds and vines grow only in gaps of light into structured forest, I take into account three basic assumption: i) the carrying capacity of the vines in an untouched forest (values of  $h$  close to  $h_{max}$ ) is, essentially, zero; ii) weeds, vines and climbers cannot grow after a clearcutting, indeed there is evidence that the forest returns to its natural composition after such management. So I assume a low (or even zero) carrying capacity of weed vines and climbers at  $h = 0$ ; iii) if the upper canopy of the forest is removed without damaging the lowest trees. In this case, one or more locations with enough light will appear at the lower levels of the forest, without shattering the vertical structure. Therefore, I am lead to conclude that the carrying capacity of the vines has a maximum at intermediate values of  $h$ .

The above discussion leads to the following conceptual model for the coexistence of forest and vines:

$$\begin{cases} \frac{dh}{dt} = (r(h) - \alpha q)h \\ \frac{dq}{dt} = \varepsilon \left(1 - \frac{q}{K(h)}\right)q \end{cases} \quad (2)$$

where  $q$  is the biomass of vines per unit area,  $\varepsilon$  is their maximum growth rate, and the function  $K$  is the  $h$  – dependent carrying capacity of the weeds and vines, which shall be a positive function for  $h > 0$  but may be zero if  $h = 0$ . The constant  $\alpha$  determines the damping strength of the vines on the (re)growth of the forest.

### 2.2. Study sites

I collected data on vine, weed and climber densities and tree heights in tropical forests of West and Central Africa (Cazzolla Gatti et al., 2015; 2017a). In West Africa, forest plots were selected along the border between Ghana and Ivory Coast (Bia National Park and Ankasa National Park). In Central Africa, forest plots were selected within the Congo river basin, in Gabon and on the border between Cameroon and Central African Republic (Sangha Tri-National Forest).

The first study area, Bia National Park, is part of a protected area of 306 km<sup>2</sup>, which comprise 77.7 km<sup>2</sup> of the national park in the north, and 227.9 km<sup>2</sup> of Resource Reserve (where logging is permitted) in the south. The area is located in the transition zone between the southern mixed evergreen forest and northern mixed semi-deciduous forest. The average annual precipitation ranges from 1500 mm to 1800 mm and the average monthly temperatures range between 24° and 28° C, with the rainy season during the months of May, June, September and October. More than 300 plant species per hectare can be observed; species from the *Makore*, *Dahoma*, *Khaya* and *Marantis* genera are widespread.

The Ankasa Conservation Area in western Ghana is a 500 km<sup>2</sup> Wildlife Protected Area. The southern parts of Ankasa were logged from the early 1960s up to 1970s. Logging intensity was relatively low due to the low volumes of commercially valuable species available. Nini Sushien contains one of the few remaining blocks of relatively untouched forest in the country. Annual precipitation is 1700–2000 mm. Plant diversity is similar to Bia National Park is classified as wet

evergreen and Ankasa as evergreen forest.

The study area in Cameroon is bordered to the east by the Sangha River, a tributary of the Congo River, and it belongs to the Sangha Tri-National Protected Area (STN). The park covers an area of 1838 km<sup>2</sup> with an altitude ranging between 300 m and 750 m above sea level. The area consists of semi-evergreen forests, with over 300 species of trees, the largest ones including *Ceiba pentandra* (L.) Gaertn, *Terminalia superba* Engl. & Diels and members of the family *Sterculiaceae* (*Triplochiton*, *Pterygota*). The average annual precipitation is 1400 mm, with the dry season occurring from December to February.

The study area of Woleu-Ntem and Moyen-Ogoouè in the north and central Gabon cover about 1800 km<sup>2</sup>. Annual precipitation is 1750–3050 mm with almost all rain falling between October and April. There is little, if any, rainfall May–September but humidity remains high. Mean daily temperature is about 27 °C and varies little throughout the year. The vegetation is a moist and evergreen forest.

In all the study sites, the commercial tree species most commonly

harvested are *Enthandrophragma cylindricum* K. Schum, *Terminalia superba* Engl. & Diels *Triplochiton scleroxylon* Sprague and *Heritiera utilis* (Sprague) Sprague. A typical selective logging scheme includes the harvest of trees with diameters bigger than 30–100 cm and logging cycles of 15–30 years. For example, in Central Africa, the minimum diameter is 100 cm for *Enthandrophragma cylindricum*, 60 cm for *Terminalia superba* and 80 cm for *Triplochiton scleroxylon* and logging cycle is 15–30 years.

### 2.3. Plots selection and data sampling

Original data used to calibrate the model proposed here are in Cazzolla Gatti et al. (2015), Cazzolla Gatti et al. (2017a) (Table 1). To identify and outline the sample plots I performed the following protocol: i) the study areas, in three tropical African countries (Cameroon, Ghana and Gabon), were surveyed to detect each forest category (primary, secondary and selectively logged; Fig. 1); 34 plots of 500 m<sup>2</sup> were

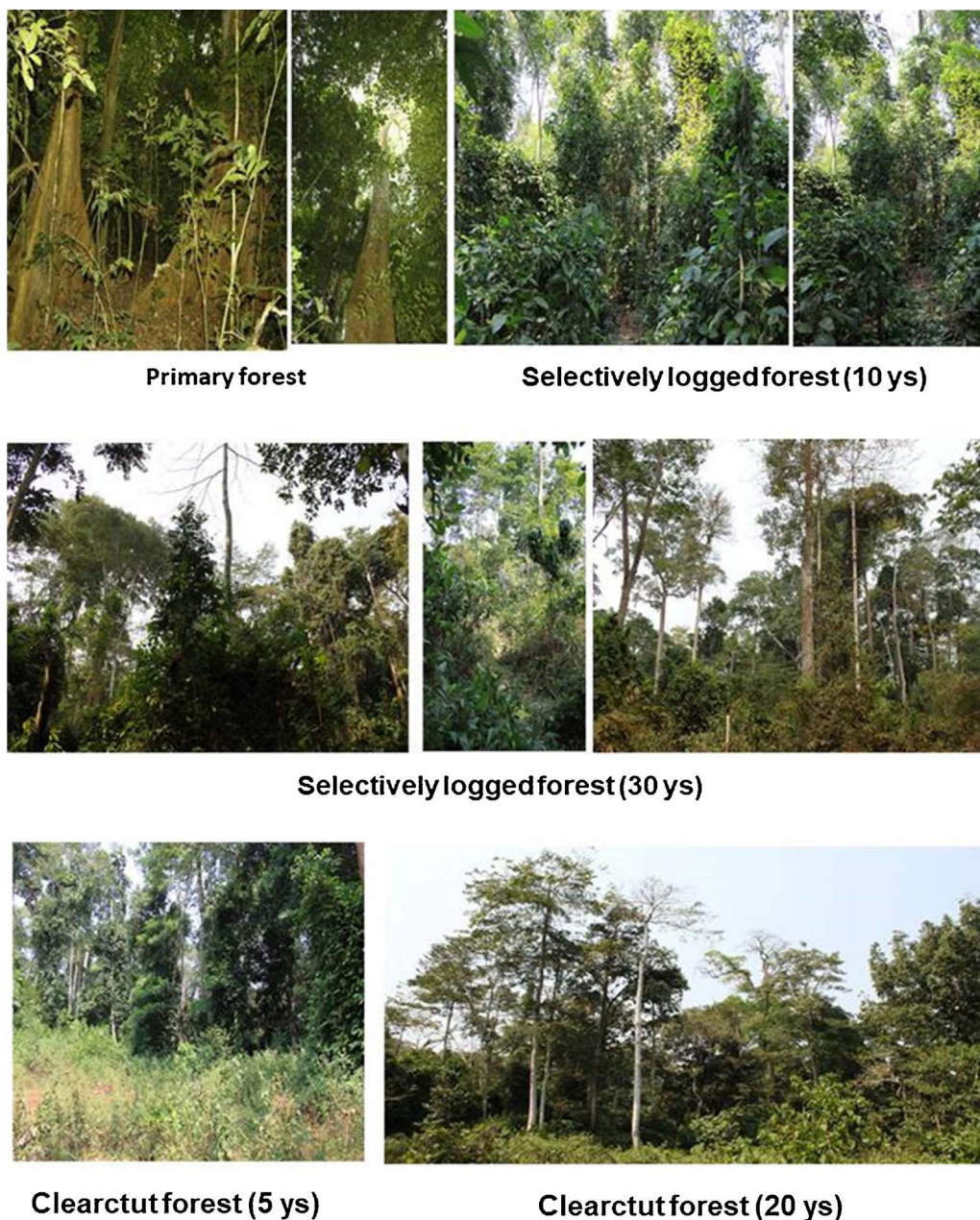


Fig. 1. Visual examples of the effect of selective logging and clearcutting (the age from the management practice is indicated in years, ys) on canopy height, forest structure and weed/vine density in some forest concessions of the south-east Cameroon (photo-credits: Roberto Cazzolla Gatti).

**Table 1**  
Study sites (plots) with their management characteristics and the related variables used to calibrate the model (weed cover, tree height and number of tree species).

Plot n°	Country (Protected Area)	Type of forest (years from the logging)	Total weed cover/ 500 m <sup>2</sup> (plot)	Mean weed cover per 100 m <sup>2</sup> (subplot)	SD weed cover per 100 m <sup>2</sup> (subplot)	Mean tree height m (plot)	SD tree height (plot)	Mean tree height (m) over 80 <sup>th</sup> percentile	N° of Tree species
1	Camerun	Primary	1	0.20	0.45	9.40	5.74	18.43	30
2	Camerun	Primary	1	0.20	0.45	12.67	8.90	29.03	23
3	Camerun	Selectively logged (logged twice)	83	16.60	3.91	10.39	8.42	24.90	22
4	Camerun	Selectively logged (20 years)	39	7.80	6.91	11.11	7.43	23.58	25
5	Camerun	Selectively logged (30 years)	95	19.00	6.63	9.00	6.07	19.25	23
6	Camerun	Secondary (clearcut 20 years)	37	7.40	7.92	9.46	6.50	19.75	10
7	Camerun	Secondary (clearcut 4 years)	7	1.40	1.14	8.50	6.50	11.50	5
8	Ghana (Bia NP)	Primary	5	1.00	1.00	8.91	8.44	21.83	38
9	Ghana (Bia NP)	Primary	5	1.00	1.00	10.69	10.32	27.78	23
10	Ghana (Bia NP)	Selectively logged (20 years)	78	15.60	1.67	10.12	6.99	22.45	33
11	Ghana (Bia NP)	Selectively logged (30 years)	158	31.60	6.84	9.95	6.27	20.18	25
12	Ghana (Bia NP)	Secondary (clearcut 20 years)	57	11.40	6.54	8.69	6.40	19.64	25
13	Gabon	Primary	2	0.40	0.55	12.90	7.67	25.69	41
14	Gabon	Primary	2	0.40	0.55	13.31	6.91	24.75	31
15	Gabon	Primary	5	1.00	1.41	12.90	7.98	27.44	29
16	Gabon	Secondary (clearcutted 40 years)	39	7.80	4.82	12.55	5.16	19.18	28
17	Gabon	Secondary (clearcutted 40 years)	53	10.60	4.16	11.12	5.26	18.83	26
18	Gabon	Secondary (clearcutted 40 years)	47	9.40	2.30	12.09	7.12	23.00	23
19	Gabon	Selectively logged (5 years)	87	17.40	5.73	11.42	5.42	21.00	20
20	Gabon	Selectively logged (5 years)	111	22.20	5.63	13.60	6.00	20.14	15
21	Gabon	Selectively logged (15 years)	117	23.40	5.13	11.50	6.64	21.30	29
22	Gabon	Selectively logged (15 years)	170	34.00	17.25	11.42	5.42	21.00	25
23	Ghana (Ankasa WR)	Primary	0	0.00	0.00	12.03	5.57	21.00	38
24	Ghana (Ankasa WR)	Primary	1	0.20	0.00	13.75	5.99	22.82	32
25	Ghana (Ankasa WR)	Primary	1	0.20	0.45	12.92	6.02	22.80	26
26	Ghana (Ankasa WR)	Primary	0	0.00	0.00	12.93	5.69	21.13	33
27	Ghana (Ankasa WR)	Selectively logged	96	19.20	7.66	9.47	5.83	19.01	21
28	Ghana (Ankasa WR)	Selectively logged	90	18.00	15.44	10.45	4.29	17.06	23
29	Ghana (Ankasa WR)	Selectively logged	84	16.80	10.03	9.61	4.24	16.64	22
30	Ghana (Ankasa WR)	Selectively logged	95	19.00	12.73	10.78	6.60	21.64	20
31	Ghana (Ankasa WR)	Secondary (clearcut)	75	15.00	20.57	10.58	5.08	18.52	24
32	Ghana (Ankasa WR)	Secondary (clearcut)	16	5.00	7.28	12.06	7.70	27.46	22
33	Ghana (Ankasa WR)	Secondary (clearcut)	88	17.60	3.85	11.74	6.04	21.19	12
34	Ghana (Ankasa WR)	Secondary (clearcut)	84	16.80	5.36	10.52	4.83	17.88	12

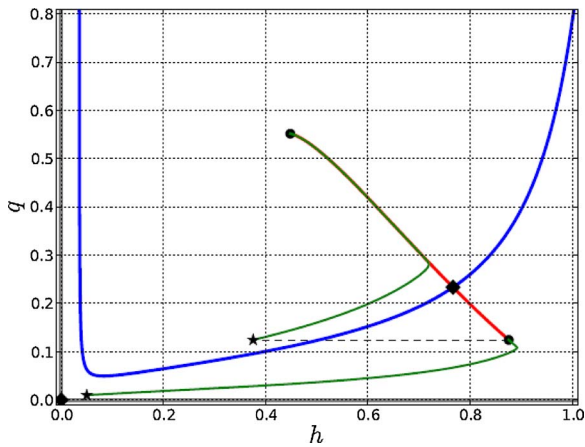


Fig. 2. Phase space model 2 for the case of solid magenta line in Fig. 3. Unstable equilibria are marked with a black square and stable equilibria with a black dot. The equilibrium corresponding to intermediate forest height and intermediate vine density is a saddle. See the text (“Data Analysis”) for more details. (For interpretation of the references to colour in text, the reader is referred to the web version of this article).

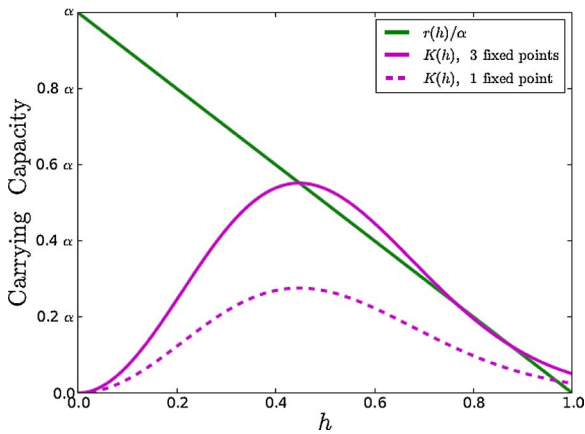


Fig. 3. Non-trivial equilibria of model 2 are determined by the intersection of the rescaled forest growth rate  $r(h)/\alpha$  (solid green line) and the carrying capacity  $K(h)$  of the weeds (solid and dashed magenta lines). Two examples are shown: i) the solid magenta line is a case where the vines’ carrying capacity is high enough at intermediate values of  $h$  as to have three non-trivial equilibria; ii) the dashed magenta line is a case where there is only one non-trivial equilibrium, attained at almost full forest height and very low weed cover. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

selected at a minimum buffer distance of 50 m from access roads and logging trails and subdivided into 5 subplots of 100 m<sup>2</sup> for an easier tree mapping and detection. The selected plots included 11 primary old-growth forests (PF), 13 areas subject to selective logging (SL) and 10 secondary forests, i.e. subject to clear-cutting and then left to recover (SF); iii) in each plot corners coordinates were collected with a GPS and the years from the last logging activity was recorded when available. Height and biodiversity variance were calculated for each of the 3 main forest management types grouping plots with similar conditions as reported in Table 1.

For each plot, I also recorded genus/species name, tree position into the plot and trees height by a laser hypsometer-dendrometer.

### 3. Results

#### 3.1. Data analysis

The evidence of the leading role of taller trees on forest structure is shown in Fig. 2. In this figure, the model’s two unstable manifolds (solid red lines) connect with the two stable equilibria. The model’s two stable

manifolds (solid blue lines) come from infinity. One of them goes close to the trivial equilibrium, without reaching it. Two initial conditions (black stars) belonging to two separate basins of attractions are shown, together with the orbits originating from them (thin solid green lines). The thin dashed black line represents the process of removing the highest, commercially-valuable trees, bringing the system from the healthy forest state (lower right black dot) to a state (the star further from the origin) which has essentially the same weed density, but a much lower value of  $h$ , and that belongs to the attraction basin of the unhealthy forest (upper left black dot). A forest fire would destroy both forest and weeds, moving the system to a state (the star closer to the origin) which is still in the basin of attraction of the healthy forest fixed point.

The standard deviation of the mean canopy height of the untouched forests (green markers) is higher than those subject to selective logging (red markers), that is, the untouched forests show greater variability in the distribution of heights.

With regard to the basic assumption of the model listed above, the data collected give rise to my hypothesis: the correlation between the average of trees height over the 80<sup>th</sup> percentile and weeds/vines/climbers is quite strong in plots subject to selective logging but not for those subject to clearcutting. In forests subject to clear cutting the weeds/vines/climbers are almost absent, indicating that they do not have important ecological roles in deforested site.

Also, the correlation between the mean canopy height and weeds/vines/climbers, although less strong, is not deniable in the plots subject to selective logging. This result is reasonable since the arithmetic mean takes into account all trees present into the plot and in tropical forests the tallest tree is also the rarest one.

#### 3.2. Equilibria

The system of Eq. (2) has the trivially fixed point  $h_0 = q_0 = 0$ , corresponding to the absence of both forest and vines. Other fixed points satisfy the following algebraic equation:

$$q_0 = K(h_0) = \frac{r(h_0)}{\alpha} \tag{3}$$

In other words, an equilibrium occurs when the growth rate of the forest, rescaled with the damping term  $\alpha$  equals the carrying capacity of the vines (Fig. 2).

On the other hand, if the upper canopy of the forest is removed without damaging the lowest trees, many more gaps with enough light will appear at the lower levels of the forest, without damaging too much the quality of the soil. Therefore, I am lead to conclude that the carrying capacity of the vines has a maximum at intermediate values of  $h$ .

Depending on the shape of the functions  $K$  and  $r$ , the condition of the Eq. (3) may be satisfied never, once, or more than once. Fig. 3 shows a case with one non-trivial equilibrium (dashed magenta line), and a case with three non-trivial equilibria (solid magenta line). For simplicity, I have used  $r(h) = (1 - h)$  and  $K(h) = \beta h^2 e^{-\gamma h^2}$ , with suitable values of the constants  $\beta, \gamma$ . If my assumptions on the general shape  $r$  and  $K$  are correct, three intersections should be not uncommon. This is the interesting case of my discussion. When there are three non-trivial equilibria, linear stability analysis shows that the equilibrium having intermediate values of  $h_0$  and  $q_0$  is unstable, and, in particular, it is a saddle. The equilibria having low  $h_0$  and high  $q_0$  (unhealthy forest with a dominance of weeds and vines), and high  $h_0$  and high  $q_0$  (healthy forest with few vines), are stable. The phase state of the system is partitioned into two basins of attractions by the stable manifold of the saddle equilibrium (the U-shaped blue line in Fig. 2). All the orbits starting from the states into the “U” region of the phase space converge to the unhealthy forest equilibrium, and the orbits from the states outside that region converge to the healthy forest state. The particular choice of  $r$  and  $K$  does not affect much this partitioning, as long as there are three non-trivial equilibria (two stable ones, and a saddle in

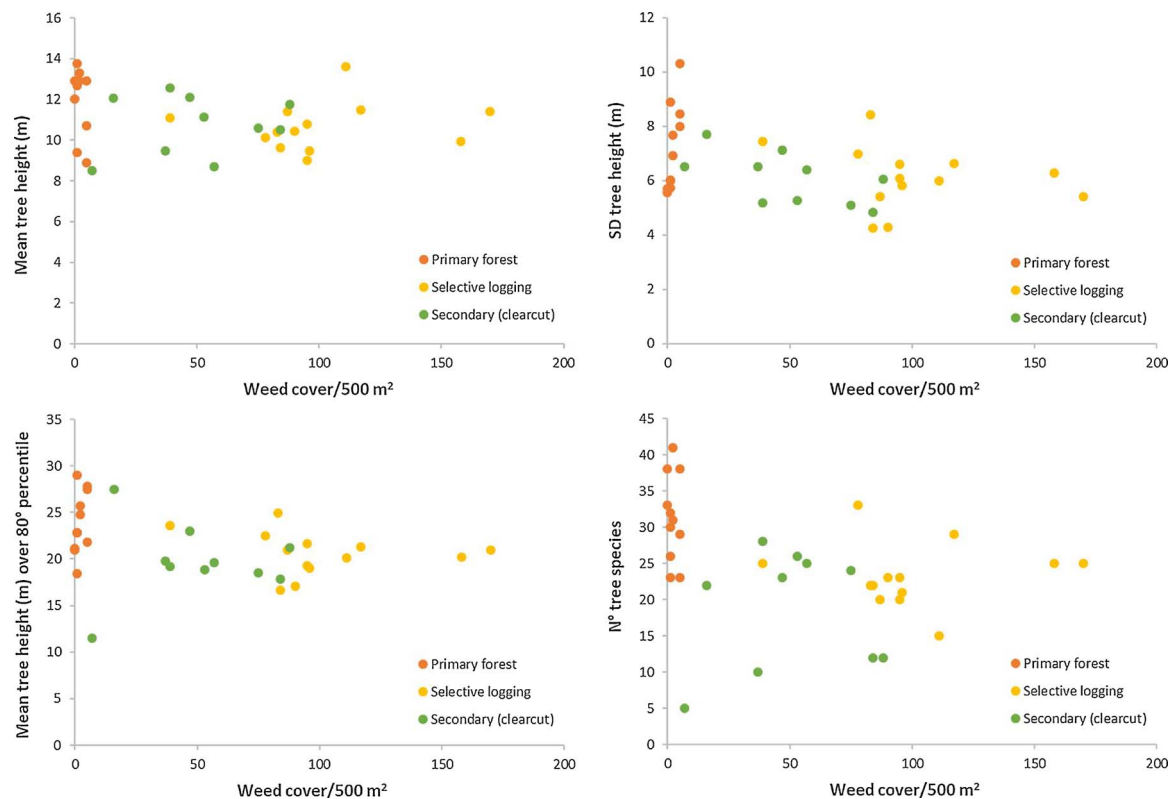


Fig. 4. Plots of the mean canopy height (m), s.d., mean over the 80<sup>th</sup> percentile and tree species number vs. weed cover/500 m<sup>2</sup>.

between them), and that  $K(0)$  is sufficiently small. If  $K(0)$  has a sufficiently high value, I have numerical evidence that a global bifurcation occurs, in which the left-side branch of the stable manifold of the saddle point originates from the trivial fixed point rather than from infinity. In this case, the states with low values of  $h$ , but a sufficiently high value of  $q$  will originate orbits converging to the unhealthy forest fixed point.

#### 4. Discussion and conclusion

The action of cutting the highest trees leaves the forest with a much-lowered value of  $h$  but changes little the density of the few vines present in the healthy forest. In other words, the cut moves the system along the horizontal dashed line in Fig. 2. If the drop in  $h$  is large enough, the new state (represented by the star at the left end of the dashed line), may belong to the basin of attraction of the unhealthy forest state. Therefore, as time passes, the forest does not recover to a healthy state but falls into the unhealthy, vine-infested one. It is possible that even the removal of a single big tree is enough to locally move the system to the unhealthy forest basin of attraction (by locally, I mean on a surface of a few thousand square meters). The possibility of recovery, then, depends on the ability of the surrounding healthy forest to invade the unhealthy spot. This calls for an explicit spatial modelling. On the other hand, the action of a fire, or other catastrophic events that destroy most of the biomass in the forest, including the vines, moves the system close to the origin (the star in the lower left corner of Fig. 2).

Because of the basin of attraction of the unhealthy forest fixed point does not extend up to the axis  $h = 0$  (it is U-shaped) all states having sufficiently small  $h$  belong to the basin of attraction of the healthy forest fixed point. From the empirical data collected on canopy height and plant diversity (Fig. 4), I have the evidence of a decreasing tree diversity in tropical forests subject to selective logging in comparison with to the same but untouched forests.

I now have evidence that there is a well-defined correlation between canopy height and biodiversity (Cazzolla Gatti et al., 2017b) and it is clear that the highest levels of biodiversity reside in the untouched

forests (Cazzolla Gatti et al., 2017c). Therefore, this finding calls for an urgent response aimed at protecting and enhancing the forest conservation through specific interventions, both in terms of policy and management and regulatory mechanisms, to prevent human pressure on tropical areas (Cazzolla Gatti, 2016c), also in the light of the recent anthropogenic impacts of climate change (Battipaglia et al., 2015). My work confirms the importance of using dynamic, deterministic models for identifying vulnerabilities and thresholds while assessing the impacts of anthropogenic activities. I believe that in the future approaches like this model will have a wider use because they provide simple and clear instruments to policy makers and planning conservation institutions.

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