



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, ε 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 α 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 km², which comprise 77.7 km² of the national park in the north, and 227.9 km² 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 km² 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

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