

Full Length Research Paper

Status of Hagenia forest in the Parc National des Volcans, Rwanda: A review of historical records

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Hagenia-shaped habitat is an important element in conservation of world's only population of mountain gorillas surviving in the wild. In fact, in the Parc National des Volcans (henceforth PNV), gorillas spend most of their life time in the nutritious herbaceous habitats near or within the Hagenia-Hypericum zone. Unfortunately, populations of *Hagenia abyssinica* in this park have been reported to be ageing. Using information drawn from the statistical analysis of records in herbaria and the cross-examination of the literature, the status of Hagenia forest in PNV is discussed. The results show that *H. abyssinica* in PNV has an unusual pattern of population structure and distribution, seemingly since many decades. No record of *H. abyssinica* was collected from PNV, but patterns of collections of *H. abyssinica* are globally similar to those of a set of five control tree species, such that this absence of records from this park cannot be considered as due to collector or collection site-bound bias. The paper ends by giving insight on possible implications for conservation of the park's wildlife, chiefly the gorillas.

Key words: Tree regeneration, herbarium records, afro-montane forest.

INTRODUCTION

Hagenia abyssinica is a typical example of an afro-montane tree endemism, now considered as endangered (Feyissa et al., 2007a). Not only it is among the rare dioecious tree species (Vamosi and Vamosi, 2005), but also is one of the few tropical rain forest tree species whose pollination and seed dispersal is mediated by wind (Turner, 2001). In the few remnant afro-montane forests where it occurs in Rwanda, *H. abyssinica* is associated with a rich and unique biodiversity such that any threat to its normal dynamics may affect the wellbeing of many wildlife species. Hagenia-shaped habitat is an important element in conservation of world's only population of mountain gorillas surviving in the wild (Sarmiento et al.,

1996). According to McNeilage (2001), corroborated by Kayijamahe (2008), gorillas in PNV were found to spend most of their life time in the nutritious herbaceous habitats near or within the Hagenia-Hypericum zone. Unfortunately, Hagenia forests seem to have been declining since many decades.

In his analysis of the vegetation structure in Denkoro forest (Ethiopia), Ayalew (2003) noticed that *H. abyssinica* had fallen in the category of those tree species whose majority of individuals was in the highest DBH (diameter at breast height) classes, suggesting that the species was no longer reproducing effectively. This result can be viewed as a validation of early

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concerns in line with which this species was declared endangered in Ethiopia (Kibebew and Addis, 1996) and the Ethiopian forestry law prohibits its utilization in this country (FDRE, 1994). In another study, Lange et al. (1997) found that on Mount Kenya, the regeneration of *Hagenia* was either decreased or abolished in areas suffering from a high herbivorous activity. Feyissa et al. (2007a) confirmed there was a reason to be concerned about the future of this species and insisted that it should be listed as endangered. *H. abyssinica* is missing on the list of 212 tree species recorded in four of the most important forests in Western Uganda [Bwindi Impenetrable National Park (BINP), Kasyoha-Kitomi Forest Reserve (KKFR), Kibale National Park (KNP) and Budongo Forest Reserve (BFR)], perhaps implying that it was too rare to be easily encountered during the survey (Eilu et al., 2004). When Eilu and Obua (2005) listed the most dominant tree species in the disturbed sites of Bwindi Impenetrable National Park, *H. abyssinica* was not included. This suggests that this species had low occurrence. Lejju et al. (2001) came up with a similar result in Mgahinga Gorilla National Park, where *H. abyssinica* was never recorded in undisturbed sites and had so-called highest frequency lower than 0.05% (=0.03).

In PNV, park amputations, which culminated in 1970s when almost all the *Neoboutonia* forest was lost to land reclamation by humans, forced gorillas to retreat back uphill to the mountains, exerting an increased pressure on vegetation and altering the course of succession within the bamboo and *Hagenia* forests (Murererehe, 2000; Nsanzurwimo, 2004; Plumptre, 1993). In addition, poaching activities further confine gorillas to the area between mounts Karisimbi and Sabyinyo, reducing their range to only a small portion of the originally suitable space. Indeed, gorilla density negatively correlates with total combined signs of human disturbance, and few gorillas are found in the area of Mikeno, south of Karisimbi and in the Eastern part of the Virunga Range (Gray et al., 2005; Kayijamahe, 2008). In fact, as it appears in the literature, *Hagenia* forest, which, unfortunately, seems to have been receding for decades, is critical to gorilla conservation in PNV and there is a reason to be concerned should this trend continue. However, due to budget constraints researchers in developing countries are inherently faced with, no other study has been so far dedicated to elucidating this problem. Not even a literature review.

This paper uses information drawn from the statistical analysis of records in herbaria and the cross-examination of the literature to discuss the status of *Hagenia* forest in PNV and some of its possible effects on the conservation of biological diversity in this park. It forms a baseline for future investigations on the causes and implications of *Hagenia* forest dynamics not only in des Parc National des volcans (Rwanda), but also in other afro-montane forests of East Africa.

MATERIALS AND METHODS

Study area

The study was conducted in Rwanda, a small landlocked country in central Africa, located around 2°00' South latitude and 30°00' East longitude. The areas concerned by this study are situated in the western and northern parts of the country, on both sides of the Congo-Nile ridge (1600-2900 m) and south to the crest line of the volcanic cones (2300-4500 m). The entire area of study is located in the Albertine Rift, a biodiversity hotspot with many endemic and endangered species (Plumptre et al., 2007). In particular, the virunga volcano range is home to world's only population of mountain gorillas surviving in the wild (Weber and Vedder, 1983). Because of high altitude, the temperature (11-18°C) and rainfall (1700-1800 mm) in the study area are more moderate than the surrounding hot and humid equatorial regions, even though the climate follows the same annual cycles.

Previously disturbed (and undisturbed) areas investigated here are located on the foothills of Muhabura Mountain, in the eastern part of des Parc National des Volcans (Figure 1). The presence of plowing or digging vestiges on the ground, burn tracks on trees or disturbance indicator species [either native (*Pteridium aquilinum*), exotic (*Eucalyptus maidenii*, *Erythrina abyssinica*, *Carica cundinamaricensis*, *Solanum tuberosum*, *Buddleja davidii*, *Setaria* sp.), or ruderal (*Galinsoga parviflora*, *Crotalaria recta*, *Solanum nigrum* and *Oxalis corniculata*)] have served as a convincing mark of disturbance (Seburanga, 2007). Undisturbed plots were defined within areas free of disturbance indicators.

Study material

Hagenia abyssinica (Bruce) Gmel. [Rosaceae] is the species of interest [or treatment, in the language of inferential statisticians] for this study. Five other tree species were selected to serve as a source of control data. These are: *Erica arborea* L. [Ericaceae], *Hypericum revolutum* Vahl. [Hypericaceae], *Dombeya goetzenii* K.Schum. [Sterculiaceae], *Arundinaria alpina* K. Schum. [Poaceae] and *Neoboutonia macrocalyx* Pax. [Euphorbiaceae]. *H. revolutum* was chosen because it is often associated with *H. abyssinica* (Table 1). *D. goetzenii*, *A. alpina*, and *N. macrocalyx* were picked for they are key tree species of the outer forest ring that envelops the *Hagenia*-*Hypericum* zone. *E. arborea* was selected as the most characteristic of the inner forest layer.

The *Hagenia*-*Hypericum* woodland, which lies between 2800-3200 m of altitude, forms the most striking forest formation. At lower altitude, it is buffered by a bamboo belt (the structure is very apparent on the western side of Karisimbi volcano and around Sabyinyo) or by a mixed forest dominated by *Dombeya* trees on the southern part of Bisoke or by a *Neoboutonia*-dominated forest on the western side of Mikeno volcano). At higher altitude (3200-3600 m), the *Hagenia*-*Hypericum* forest is replaced by a heather land, which forms the uppermost woody vegetation (Watts, 1983). In total, there are five to nine vegetation strata (Steklis et al., 2005). However, for the sake of simplicity, this study was limited to the description of those directly connected to the *Hagenia* forest, with their respective key tree species (*Hagenia*, on the one hand, and the five control tree species, on the other hand). The total number of vegetation formation in PNV varies with the research objectives and the methods used for classification.

Specimens whose collection dates were not specified [for example, Specimen No 2044 of *D. goetzenii* by Ewango and Specimen No 225 of *N. macrocalyx* by Nuyt C.] were removed from the analyzed sample. For any species represented by many copies of specimens, only one copy was retained for the analysis, if four conditions were fulfilled; that is, if all copies were collected (1) at the same location (2) during the same year and (3) by the same person

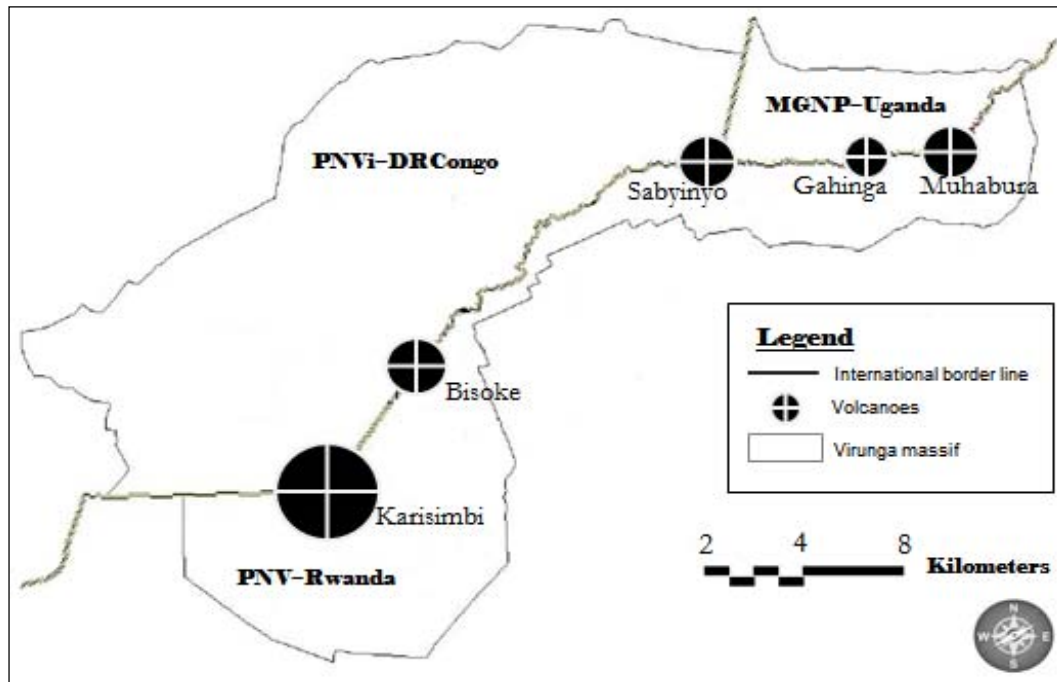


Figure 1. Location of the Parc National des Volcans (PNV) in the virunga massif.

Table 1. Sample species per Hagenia-associated vegetation zone.

| Vegetation type | Characteristic tree species | Altitude (m) |
|----------------------------|--|--------------|
| Sub-Alpine | <i>E. arborea</i> | 3200-3600 |
| Hagenia-Hypericum woodland | <i>H. abyssinica</i> , <i>H. revolutum</i> | 2800-3200 |
| Bamboo forest | <i>A. alpina</i> | 2500-2800 |
| Mixed forest | <i>N. macrocalyx</i> , <i>D. goetzenii</i> | 1600-2500 |

and (4) were assigned the same specimen number. This was the case for Specimen No 869 of *D. goetzenii* collected by Bouxin (1971) from Mayebe site and Specimen No 15385 of *D. goetzenii* collected by Troupin (1974) from Gikungu location, which had two copies each. With regard to the two duplicates of Hagenia record No 22, both taken at exactly same geographical coordinate (UTM 0758465/9724490) in 1990 from Rubyiro location by two different collectors [Ferdinand and Ngayabahiga], we suspected that there was inconsistency in recording the collector’s name (one, the forename and, the other, the surname of same person) and presumed they were just two copies of same record by Ferdinand Ngayabahiga; thus treated as such.

Records of different infra-specific taxa that belong in a same species were grouped into one set and considered as mere copies of that species. This was the case for *H. revolutum* whose data comprised three different entries: *Hypericum revolutum*, *Hypericum revolutum* (trois), and *Hypericum revolutum* Vahl. They were treated as copies of a same species and assigned one entry name: *Hypericum revolutum* Vahl.

Spelling or nomenclatural errors were corrected based on our expert judgment. For instance, the entry name *Harundinaria alpina* of specimen no. 674 collected by Nzakizwanayo (2005) from Mukura forest was treated as another specimen of *A. alpina*. Except where indicated otherwise, taxonomic classification and species

nomenclature used in the database were maintained, for the sake of easy comparison. Among taxa treated as such is *Arundinaria alpina*, a species whose nomenclature has evolved a lot since the time the first collections were made. It once was referred to as *Arundinaria alpina* K. Schum. (Owiunji et al., 2004), then as *Sinarundinaria alpina* (K. Schum.) C. S. Chao & Renvoize (Nsazurwimo, 2004; Karlowski, 2006), and since recently as *Yushania alpina* K. Schumann Lin. (Ohrn) (Seburanga, 2007). Only the name *Arundinaria alpina* K. Schum., as used in the plant database at National Herbarium of Rwanda, is hereafter applied when referring to this taxon.

Data collection

The study builds upon raw data of three kinds: Field-drawn data (tree DBH data), herbarium records (historical occurrence data), and literature-extracted data (spatial occurrence maps).

Number of Hagenia trees per DBH class

Data on Hagenia tree distribution per DBH class were collected in 2007 on the foothills of Muhabura Mountain in the Parc National

Table 2. Number of *Hagenia* individual trees per DBH classes on Muhabura Mountain, Parc National des Volcans [data extracted from Seburanga (2007)].

| Type of site | DBH (diameter at breast height) classes | | |
|--------------------|---|------------|---------|
| | ≤ 10 cm | 10 - 30 cm | ≥ 30 cm |
| Disturbed forest | 2 | 1 | 1 |
| Undisturbed forest | 2 | 2 | 4 |
| Total | 4 | 3 | 5 |

des Volcans, between 2500 and 3300 m of altitude (Seburanga, 2007). These data were collected along four transects, each passing across two neighboring areas (disturbed and undisturbed area), by the plot method and semi-stratified sampling. Circular plots of 20 m in radius were established at every 250 m interval along the reconnaissance trails. In total, 44 plots equitably distributed between disturbed and undisturbed areas were surveyed. Each pair of sites was characterized by comparable topography, altitude average, soil nature and vegetation type for valid comparison. Height and DBH (diameter at breast height) was measured for individual trees occurring in a plot.

Hagenia historical occurrence in Rwanda

To assess whether its arrested regeneration, as suggested by findings of contemporary studies, is not merely a recent trend or a temporary event with no lasting effects, we delved into herbarium records of *Hagenia* in Rwanda to analyze its historical patterns of occurrence [for the appropriateness of use of herbarium records in ecological studies please refer to Fuentes et al. (2013) and Antonovics et al. (2003)]. Species record counts and associated data, including collection dates and names of sites and collectors, were drawn from the plant database available at the National Herbarium of Rwanda, hosted at the Rwanda Institute of Scientific and Technological Research (IRST). Historical occurrence data were retrieved for five other tree species to serve as control data, to measure the likelihood that the observed trend is not simply due to a species or collector-bound bias that might originate from collectors' differential effort to take record of *Hagenia* in PNV as compared to other parks. Cross-references to the records were retrieved from databases of Botanical Garden Meise (Belgium) and Kew Gardens (UK).

Hagenia spatial occurrence in the virungas

To assess whether its reported arrested regeneration is just a PNV-bound problem or a transboundary issue whose fallouts extend to the entire virunga massif, data on *Hagenia* presence/absence in the virungas were extracted from Owunji et al. (2004), Dondeyne et al. (1993), McNeilage (1995), Nsanzurwimo (2004), Steklis et al. (2005) and Seburanga (2007) in order to analyze patterns of its spatial occurrence in the three contiguous parks: Parc National des Volcans (Rwanda), Mgahinga Gorilla National Park (Uganda), and Parc National des Virungas (Democratic Republic of Congo).

Data analysis

Number of *Hagenia* trees per DBH class

For both the disturbed and undisturbed forest, DBH data were stratified into three categories: ≤ 10, 10 < x < 30 and ≥ 30 cm. Analysis was conducted through simple scree plotting, using filter and sorting tools of Microsoft excel applications.

Hagenia historical occurrence in Rwanda

Herbarium data were stratified into two data sets based on the parent material of the dominant soils under the forests from which the specimens were collected: [A] Collections taken from forests on both sides of the Congo-Nile ridge (shale, micaschist, micaceous granite, quartzitic or granitic rock) and [B] Collections taken from virunga massif forest (volcanic rock) (Verdoodt and Van Ranst, 2003).

Hagenia spatial occurrence in the virungas

Data on presence/absence of *Hagenia* (and of five control species) were selectively retrieved, noting whether the species was Albertine Rift Endemic (ARE) or IUCN-red listed as vulnerable. A data matrix was created based on a binary coding system in which "1" stands for species presence and "0" for species absence.

The normality of data was assessed using the Shapiro-Wilk test. Paired Sample Wilcoxon Signed Ranks Test was used to assess the level of significance of differences between record counts from the Congo-Nile ridge and virunga massif samples. Pearson Correlation Test allowed the quantification of co-variation observed between species record counts, number of collection campaigns (expressed in term of different years the specimens were collected) and number of collectors onboard.

RESULTS

Number of *Hagenia* trees per DBH class

The results show that *Hagenia* trees are very rare in Muhabura forest (Table 2), especially larger trees (DBH ≥ 30 cm) within previously disturbed areas. Sites combined, there are more trees within the ageing class (DBH ≥ 30 cm) than in younger categories.

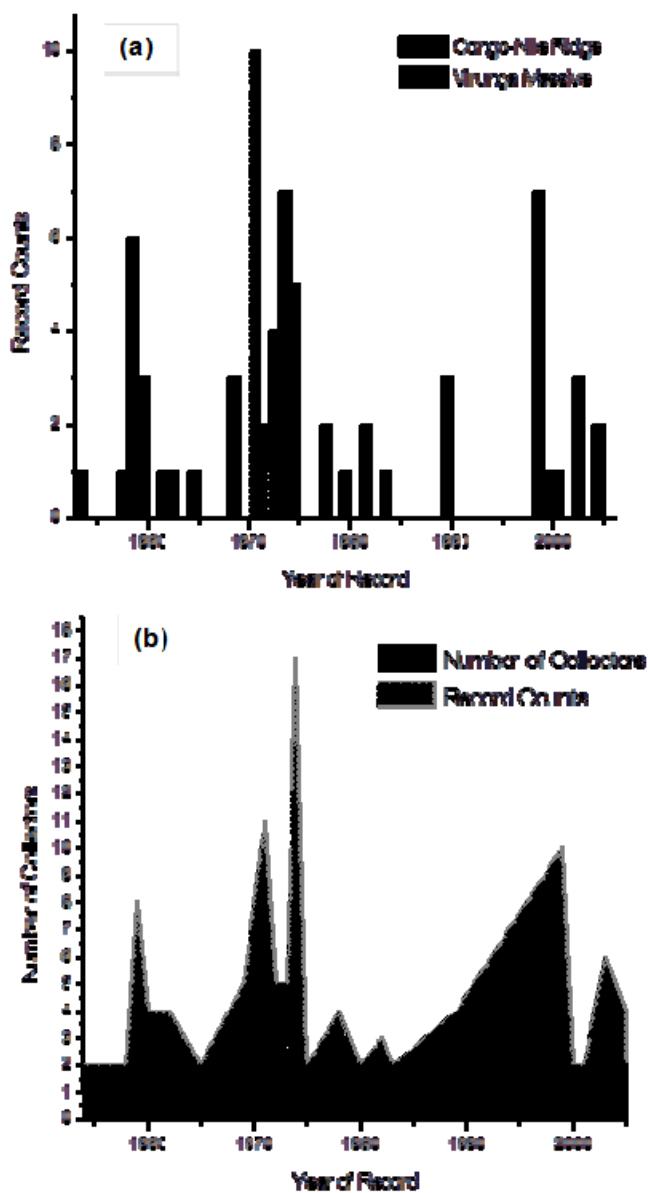
Hagenia historical occurrence in Rwanda

All records of *Hagenia* were taken from areas beyond the virunga massif (from forests on both sides of the Congo-Nile ridge). Around 66.7% of the total number of the specimens were collected from Nyungwe National Park only (Table 3).

When records of *H. abyssinica* and those of control tree species were combined, statistical analysis showed a difference between record data series from Congo-Nile ridge forests or nearby and virunga massif or close areas ($W = 210.5$; $Z = 3.32$; $Prob > |W| = 3.233E-4$) (Figure 2a). The majority of specimens (84 %) were collected in areas

Table 3. Historical records of *H. abyssinica* in Rwanda.

| Collector | Number | Location | Region | Date | Altitude | Habitat |
|-----------------------|--------|-------------|-----------|------|----------|-----------------------|
| Troupin G. | 15268 | Gikungu | Gisenyi | 1974 | 2150 | Disturbed forest |
| Troupin G. | 10474 | Uwinka | Cyangugu | 1959 | 2300 | Forest hillside |
| Troupin G. | 10403 | Unspecified | Cyangugu | 1959 | 2360 | Forest hillside |
| Bouxin G. & Radoux M. | 830 | Mugasare | Cyangugu | 1969 | 2300 | Riparian and roadside |
| Troupin G. | 14735 | Wisumo | Kibuye | 1973 | 2200 | Disturbed forest |
| Reynders | 373 | Rutovu | Gikongoro | 1959 | 2400 | Valley forest |
| Bouxin G. | 1036 | Mugasare | Cyangugu | 1971 | 2400 | Riparian forest |
| Nzakizwanayo E. | 12 | Uwasenkoko | Gikongoro | 1999 | 2370 | Open forest |
| Ngayabahiga | 22 | Rubyiro | Gikongoro | 1999 | 2170 | Open forest |

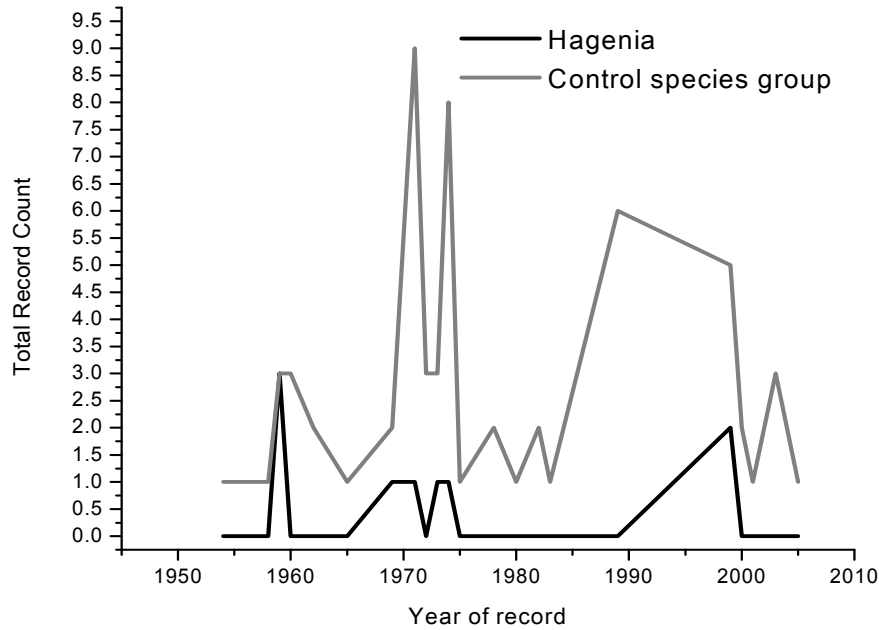
**Figure 2.** (a) Species record per sites and (b) per plant specimen collector.

areas beyond the virunga massif. On the other hand, record counts correlate with the number of collectors ($r^2 = 0.652$; $p < 0.001$) (Figure 2b).

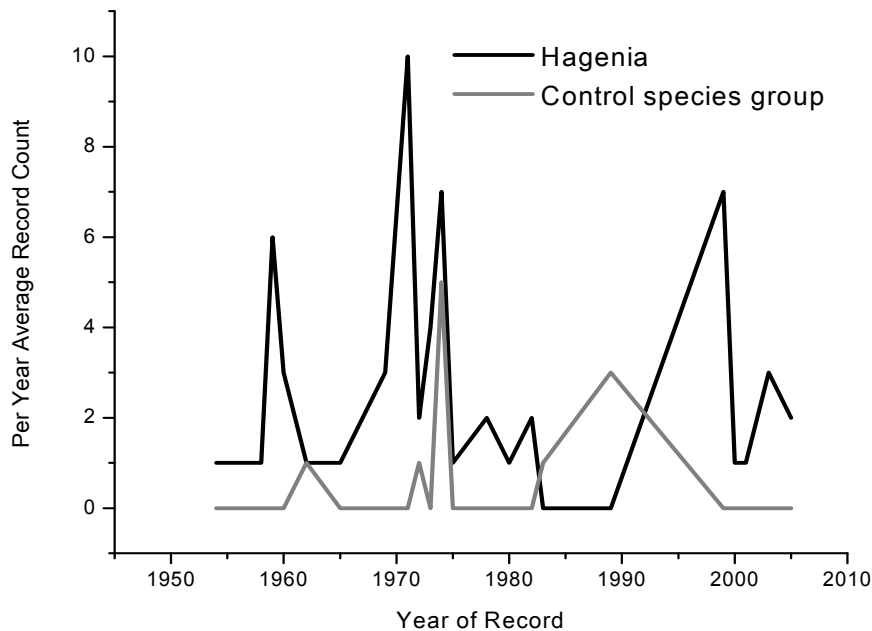
Roughly 67.14% of the specimens were collected by 1975. *H. revolutum* was as the most regularly collected, accounting for 31.4% of the records, with only 13.6% of its records taken from PNV or close areas. Both *H. abyssinica* and *N. macrocalyx* were never collected from PNV or close areas. For unknown reasons, records of *H. abyssinica* and the five control tree species occurred in a series of waves of collection [refer to the four in-phase collection peaks in 1959, 1971, 1974, and 1999, respectively (Figure 3b)] and the specimens taken in a given collection period appeared to be restricted to one or two collection sites (Table 3). A similar pattern of specimen collection was detected at the regional scale, suggesting that the earliest record of *H. abyssinica* in Rwanda was taken during late 1950s, more than 4 decades it was recorded in the Democratic Republic of Congo by Bequaert (in 1914) [note that an even earlier record was taken in this country by Schimper in 1838 (Botanical Garden Meise, 2014)]

There is an apparent similarity of trends for the two distributions, with four parallel peaks in 1959, 1971, 1974, and 1999. However, a paired Wilcoxon Signed Ranks Test revealed that the two distributions are significantly different ($W = 0$, $Z = -4.04$; $Prob > |W| = 9.536E-7$) (Figure 3a). When the test was performed using *Hagenia* record counts and Control species *yearly average* record count [total count for the group divided by the number of species in the group], the two distributions were found to be not significantly different ($W = 68.5$, $Z = -1.88$; $Prob > |W| = 0.056$) (Figure 3b), suggesting that the previously observed difference was due to the fact that the cumulative number of record counts for the group of control species was obviously higher than the record counts of a single species, *Hagenia*.

Roughly 2/3 of records were taken by not more than five specimen collectors. Only two collectors, Troupin G. and Bouxin G., accounted for 42.8% of the records (Table 4). Per collector intervention time ranges from one



a)



b)

Figure 3 (a and b). Evolution of record counts per tree species (*Hagenia*) or group of species (the five control tree species combined).

to seven years. A strong relationship was observed between the number of records per collector and the number of concerned species ($r^2 = 0.868$; $p < 0.001$), on opportunity to make more records and collect a bigger number of different species.

Hagenia spatial occurrence in the virungas

Two species (*A. alpina* and *H. revolutum*) had regular occurrence in PNV as they were recorded in all sectors

the one hand, and the number of collection campaigns (different years) ($r^2 = 0.872$; $p < 0.001$), on the other hand.

Collectors that took part in more campaigns had more that fall within the boundaries of this park [Figure 4c and d (compare with Figure 1)]. They are followed by *H. abyssinica*, which occurs in all parts of PNV, except in the area between mounts Sabyinyo and Gahinga, and *D. goetzenii*, which is missing only in the extreme west. *N. macrocalyx* has the same distribution as *D. goetzenii*, with the difference that, in addition, it is missing in the area around Mount Bisoke. *E. arborea* is the rarest

Table 4. Number of specimens and species collected per collector and per year of record.

| Collector name | Record count | Number of species | Year of record |
|-----------------------|--------------|-------------------|----------------|
| Auquier P. | 1 | 1 | 1974 |
| Auquier P. | 2 | 2 | 1972 |
| Bouxin G. | 10 | 5 | 1971 |
| Bouxin G. & Radoux M. | 3 | 3 | 1969 |
| Christiaensen A.R. | 1 | 1 | 1954 |
| Etienne C. | 1 | 1 | 1972 |
| Knox E. | 3 | 3 | 1989 |
| Lewalle J. | 1 | 1 | 1965 |
| Mulindahabi F. | 1 | 1 | 1999 |
| Munyaneza E. | 1 | 1 | 2005 |
| Musabe T. | 1 | 1 | 2000 |
| Mvukiyumwami J. | 2 | 1 | 1982 |
| Mvukiyumwami J. | 1 | 1 | 1983 |
| Ndiramiye G. | 1 | 1 | 2001 |
| Ngayabahiga F. | 3 | 2 | 1999 |
| Ngayabahiga F. | 1 | 1 | 2003 |
| Ntahumwe T. | 1 | 1 | 2003 |
| Nuyt C. | 2 | 2 | 1974 |
| Nzakizwanayo E. | 3 | 3 | 1999 |
| Nzakizwanayo E. | 1 | 1 | 2003 |
| Nzakizwanayo E. | 1 | 1 | 2005 |
| Rameloo J. | 1 | 1 | 1974 |
| Raynal J. | 1 | 1 | 1978 |
| Reynders M. | 2 | 2 | 1959 |
| Reynders M. | 1 | 1 | 1958 |
| Sita P. | 1 | 1 | 1978 |
| Troupin G. | 1 | 1 | 1980 |
| Troupin G. | 7 | 4 | 1974 |
| Troupin G. | 4 | 3 | 1959 |
| Troupin G. | 3 | 2 | 1960 |
| Troupin G. | 1 | 1 | 1962 |
| Troupin G. | 4 | 2 | 1973 |
| Troupin G. | 1 | 1 | 1975 |
| Van Der Veken P. | 1 | 1 | 1962 |
| Van Der Veken P. | 1 | 1 | 1974 |

among the six.

DISCUSSION

Number of Hagenia trees per DBH class

Distribution of Hagenia individual trees within DBH classes does not show a reverse J size class distribution as expected of a properly regenerating species (White and Edwards, 2000). Instead there seem to be many more adults than saplings or seedlings [note that the number of Hagenia trees was too little to warrant a statistically unshakable conclusion, which requires us to interpret tree DBH results with reasonable caution].

Seburanga (2007) studied the regeneration of tree species in this part of the park. He found that, unlike Hagenia, the DBH profile of *Dombeya goetzenii* (one of the five control species used in this study) had a completely different shape, with more saplings than ageing trees. According to the same author, per species number of trees averaged at 106.2 and 8.2 trees for the ranges of ≤ 10 and ≥ 30 cm of girth diameter, respectively. In this study, Hagenia registered only 4 saplings with ≤ 10 of DBH and 5 individuals in the ageing class. However, this finding should be interpreted with caution because data are not presented in equal age classes. Passage time may vary a lot from size class to another. Indeed, if a tree is very long-lived, it could be perfectly sustainable to have a population with more

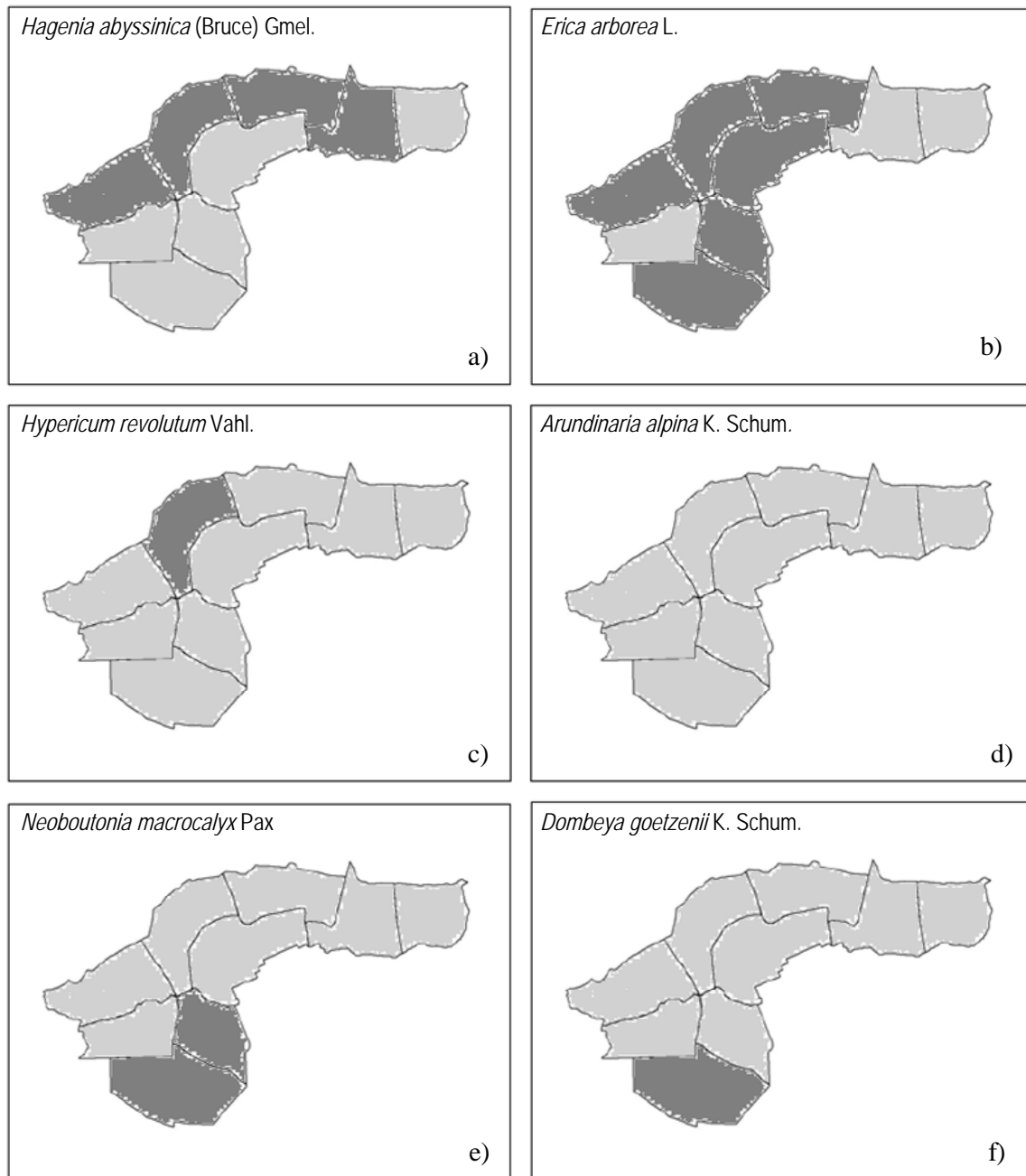


Figure 4. Occurrence of *H. abyssinica* and five other key tree species in virunga parks, including the PNV (for official boundaries of this park, please as shown in Figure 1).

adults than juveniles. For instance, if a tree takes 30 years to mature and lives for 600 years on average, with low mortality rates, a population could be stable with only a little over 30/600 or 5% juveniles. In addition, Norghauer et al. (2011) recognize that wind-mediated seed dispersal of tropical forest trees is poorly understood. Interestingly, they found that tree diameter correlated positively with increased seed shadow extent, with the bulk of seeds falling within X m from parent trees and juvenile-to-seed ratios peaking at $[X+\alpha] - [X+\beta]$ m,

where $X = 30$, $\alpha = 5$, $\beta = 15$, and $m = 1$ meter). One may infer that variables X , α , and β would vary from species to another. Note that the trees they studied were relatively isolated from each other. Relevant to the current study, one should wonder what would happen in a population of trees where the average distance between two neighbor trees is equal or less than X m. Obviously, the juvenile-to-seed peaks at $[X+\alpha] - [X+\beta]$ m would be suppressed and the number of stems within lower DBH classes significantly reduced. To insure more objectivity, further

investigation is needed to determine the average age of trees at a given DBH class and juvenile-to-seed ratios in relation to distance between neighbor trees.

Elsewhere in the region, Ayalew (2003) obtained a comparable result, suggesting that *H. abyssinica* in Denkoro forest (Ethiopia) had fallen in the category of those tree species whose majority of individuals was in the highest DBH classes. In neighboring Uganda, *H. abyssinica* is missing on the list of 212 tree species recorded in four important forests [Bwindi Impenetrable National Park (BINP), Kasyoha-Kitomi Forest Reserve (KKFR), Kibale National Park (KNP) and Budongo Forest Reserve (BFR)], implying that it was too rare to be easily encountered during the survey.

Specifically for the virungas, Lejju et al. (2001) came up with a similar result in Mgahinga Gorilla National Park, where *H. abyssinica* was never recorded in undisturbed sites and had so-called highest frequency lower than 0.05% (=0.03%) in exotic woodlots, a result that was still applicable three years later (Lejju, 2004). Karlowski (2006) indirectly corroborated these findings upon examining the soil-seed bank in four afro-montane forests in Bwindi Impenetrable National Park, along with two other Uganda's forests (Mgahinga Gorilla National Park and Echuya Forest Reserve), only to realize that, in the Hagenia-Hypericum zone, the potential for regeneration to an afro-montane forest was zero percent.

Hagenia historical occurrence in Rwanda

Although none of herbarium collections of this plant was taken from PNV, the arrested regeneration of *H. abyssinica* in PNV has been noted and reported by researchers for decades. The earliest note is that of Troupin (1980s) when he compiled his book 'Flore des plantes ligneuses du Rwanda'. Troupin is responsible for four out of the nine collections of *H. abyssinica* at the National Herbarium of Rwanda. Unfortunately, he collected none from PNV or close areas.

The analysis of herbarium records confirmed that the collection of *H. abyssinica* globally followed a usual pattern as compared with five other tree species characteristic of the vegetation in PNV (please refer to Figure 3), such that the idea of a possible link between its absence in PNV records at the National Herbarium of Rwanda and its relatively lower abundance in this park is ruled out. Herbarium records show that Botanist G. Troupin had been in that park in 1974, where he collected specimens *D. goetzenii* and *A. alpina*. Why did he not collect any of *H. abyssinica*? Perhaps, he remembered to have collected four specimens of this plant in Nyungwe (2), Kibuye (1) and Gisenyi (1) the same year, maybe during the same tour. In any case, that, in his book, he noted the absence of any sign of regeneration of *H. abyssinica* PNV (Troupin, 1982), he attests to the hypothesis that he was well aware of the dynamics of this plant in that part of the country. What about the other four

collectors of *H. abyssinica* specimens (Table 3), namely G. Bouxin, M. Radoux, M. Reynders, E. Nzakizwanayo, and F. Ngayabahiga? An examination of the entire plant database revealed that they did not collect any plant specimen of any species from PNV, suggesting that they simply did not work in that park at all.

Hagenia spatial distribution in the virungas

First reported in Troupin (1982), the absence of effective regeneration continued such that, in 1990s, seedlings and saplings of *H. abyssinica* were reported to be very rare in this park, except in few places where scattered cases of vegetative re-sprouting could be observed (Karamuka, 1993).

Steklis et al. (2005) produced an updated map of PNV vegetation. On this map, the area between Karisimbi and Bisoke (conventionally referred to as the "Karisoke" area, a name coined by late Dian Fossey) is shown in a kind of mosaic texture (Figure 5a), reflecting the existence of a more open Hagenia canopy, which aligns with Owunji et al. (2004) when they indicate that the "Hagenia-Hypericum zone forms open canopies with abundant herbaceous undergrowth". It also is in accord with the findings of Dondeyne et al. (1993), suggesting that *H. abyssinica* had a rarer occurrence (overall frequency: 5 %) as compared with *H. revolutum* (overall frequency: 41%) (Details are provided in Table 5). Interestingly, Dondeyne (1992) suggests that Hagenia canopy in that area was still closed as of early 1990s. Note that the area is represented as a long and relatively wide strip on Marius' map (Figure 5b); in contrast to the mosaic texture on Steklis et al.'s map (Figure 5a).

In their article on ranging behavior of southern tree hyrax in this park, Milner and Harris (1999) noted the uniform age structure within PNV Hagenia stands and confirmed the absence of regeneration. Owunji et al. (2004) recognized that this species was IUCN red-listed as vulnerable [note the contradiction with IUCN (2013)], but said nothing about its status in PNV. A re-examination of the data they presented yielded a result that does not conflict with the idea that the problem with this plant is not at the level of presence/absence (Figure 4), but should be addressed from a density- and dynamics-dependent aspect. With knowledge drawn from having regularly visited this park during the second half of 2000s, combined with information from colleagues that continued to work in this park to date, the authors confirm that the species is currently mostly represented by large and old trees surrounded by an ever expanding herbaceous layer (Dondeyne et al. (1993).

Insight on possible conservation implications

The frequency of gorillas out-of-park in PNV has soared

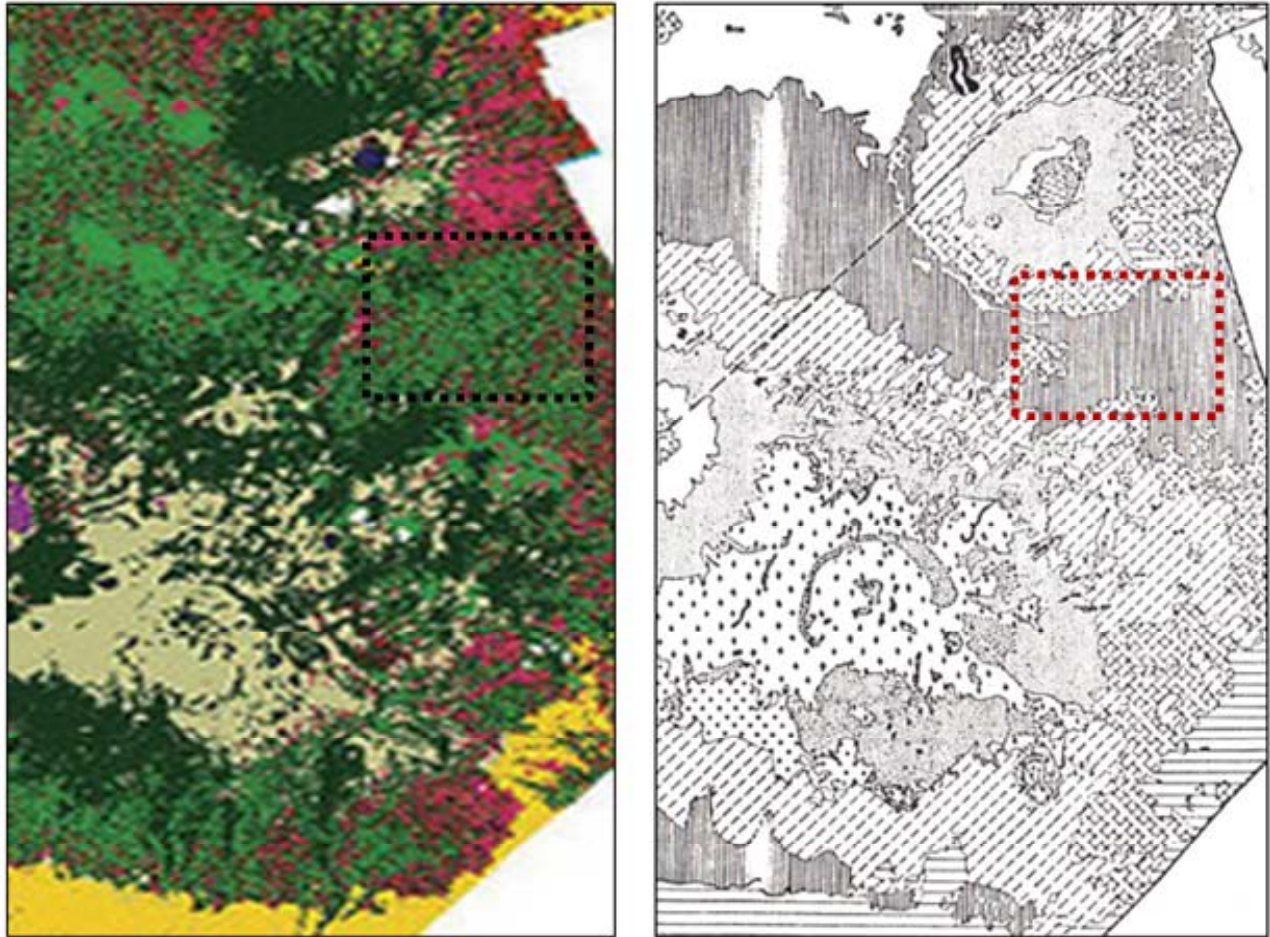


Figure 5. Evolution of Hagenia forest cover in PNV's Karisoke area (area inside black (a) and red (b) dash-edged rectangles): (a) 2000s vegetation map by Steklis et al. (2005) [area inside the black dash-edged rectangle] and (b) 1970s vegetation map by (Dondeyne, 1992) [area inside the red dash-edged rectangle].

Table 5. Presence/absence of *H. abyssinica* and *H. revolutum* in different sites around Bisoke volcano [A Paired sample Wilcoxon Signed Ranks Test yielded a result that suggests significant difference between the two distributions ($W = 1$, $Z = -2.12$; $\text{Prob} > |W| = 0.0312$) (data extracted from Dondeyne et al. 1993).

| Site ID number | <i>H. revolutum</i> | <i>H. abyssinica</i> |
|----------------|---------------------|----------------------|
| 1 | 3 | 2 |
| 2 | 0 | 0 |
| 3 | 1 | 5 |
| 4 | 1 | 8 |
| 5 | 0 | 9 |
| 6 | 0 | 7 |
| 7 | 0 | 4 |
| 8 | 0 | 2 |
| 9 | 0 | 0 |

since recently. For instance, in 2011, a group of PNV gorillas, for the first time in history, nested on adjacent farmland for two consecutive nights (DFGFI, 2011). Does

this unusual foraging behavior have something to do with the long-reported Hagenia forest arrested regeneration [or, as we prefer to call it, the unusual pattern of Hagenia population structure and distribution]? Perhaps, it is too early to establish such a causal relationship. Nevertheless, according to McNeilage (2001), corroborated by Kayijamahe (2008), gorillas in PNV [serving as the flag and umbrella species for this park (Cowlshaw and Dunbar, 2000)] spend most of their life time in the nutritious herbaceous habitats near or within the Hagenia-Hypericum zone. Mammal-forest interactions in PNV have also been established as resulting from the 1990s park amputations that caused the animals adapted to the *Neoboutonia* forest to retreat to the remaining part of the park, thus, exerting more pressure on the vegetation and altering the course of succession within the bamboo and Hagenia forests (Murererehe, 2000; Nsanzurwimo, 2004; Plumptre, 1993). Therefore, there is room to hypothesize that overgrazing and trampling of vegetation under Hagenia tree canopy may have had the effect of widening forest gaps and perpetuating the herb-

Table 6. Protection status of *H. abyssinica*.

| Species | International protection | | | National legal protection | |
|---|--------------------------|----|----|---------------------------|-----------------|
| | ARE | CP | IR | Specific-based | Ecosystem-based |
| <i>Erica arborea</i> L. | 0 | 0 | 0 | 0 | 1 |
| <i>Hypericum revolutum</i> Vahl. | 0 | 0 | 0 | 0 | 1 |
| <i>Hagenia abyssinica</i> (Bruce) Gmel. | 0 | 0 | 1 | 0 | 1 |
| <i>Dombeya goetzenii</i> K. Schum. | 0 | 0 | 0 | 0 | 1 |
| <i>Arundinaria alpina</i> K. Schum. | 0 | 0 | 0 | 0 | 1 |
| <i>Neoboutonia macrocalyx</i> Pax | 0 | 0 | 0 | 0 | 1 |

ARE: Albertine Rift Endemic, CP: CITES-protected, IUCN-red listed.

aceous physiognomy through cyclic grassy vegetation renewal, which impedes the return to a closed forest cover (Babaasa et al., 2004; Babaasa, 2009; Chapman et al., 1999; Lange et al., 1997; Paul et al., 2004; Plumptre, 1993). This effect may have been exacerbated by the fact that poaching activities, very common in the areas of Mikeno, south of Karisimbi and eastern part of the virunga massif, caused further confinement of PNV gorilla range to only a small portion of the suitable space (Gray et al., 2005; van Gils and Kayijamahe, 2009). More evidenced, the decline of southern tree hyraxes in PNV has been linked to the ever noticeable rarefaction of large and cavity-forming *Hagenia* trees, the most preferred trees for hyrax feeding and shelter in PNV (Milner and Harris, 1999; Topp-Jørgensen et al., 2008). Conversely, the decline of tree hyraxes may have had a fallout on *Hagenia* population structure (Seufert et al., 2009; Shanahan et al., 2001).

The ministerial Order No 007/2008 of 15/08/2008 establishes the list of protected animal and plant species in Rwanda (Primature, 2008). Unfortunately *H. abyssinica* was not included, perhaps because the promoters of this law had shared the view that this species is abundant in Nyungwe National Park (Fischer and Killmann, 2008; Bloesch et al., 2009) [which corroborates the opinion held by scientists at Kew Gardens assigning it the IUCN Red List Index of a "Least Concern" species (Kew Gardens, 2014)] or simply were not advised on its status in PNV and elsewhere (Owiunji et al., 2004). That this species, though already listed in its "Catalogue of Life", has not yet been assessed for the official IUCN Red Listing may suggest that it is too abundant to receive the attention of scientists who would otherwise be prompted to refer it to the IUCN Red List Authorities for consideration (IUCN, 2013). However, such reports should not distract researchers in Rwanda from the aim to investigate the problem *Hagenia* is faced with in PNV. After all, what suppresses it in PNV, if remained unidentified or not dealt with, may soon follow it also in areas where it is currently abundant.

To illuminate these relationships, there is a need to conduct extensive research on the ecology of regeneration of *H. abyssinica*, which has already begun elsewhere but in Rwanda (Feyissa et al., 2005; Feyissa

et al., 2007b). Meanwhile, this tree species should be provisionally listed as endangered in Rwanda, and possibly be included on the checklist of nationally protected species of Rwanda (please see Table 6 for updates on the current status).

Conclusion

This study established that *H. abyssinica* in PNV has an unusual pattern of population structure and distribution, seemingly since many decades ago. The earliest note of PNV *Hagenia* forest recession dates back to 1980s. Analysis of herbarium records confirmed that the collection of *H. abyssinica* globally followed a usual pattern as compared with five other tree species characteristic of the vegetation in PNV, to such an extent that the idea of a possible link between its absence in PNV records at the National Herbarium of Rwanda and its relatively lower abundance in this park is ruled out. All *Hagenia* collectors but Troupin G. appeared to have not worked in PNV at all, partly explaining why none of the *Hagenia* specimens was taken from this park. The reason why Troupin did not collect one in PNV while he collected other species [*Arundinaria alpina* K. Schum. (Specimen No 15444) and *Dombeya goetzenii* K.Schum. (Specimen No 15413)] from this park in 1974 remains an unanswered question. However, there is evidence that he was well aware of the dynamics of this plant in that part of the country. An examination of most recent references to *Hagenia* forest in PNV showed that the problem with this plant is not at the level of presence/absence, but is mostly a density- and dynamics-related issue. Because extensive research is needed before any course of field-based conservation action should be taken to deal with effects of this problem on other species, its provisional listing as endangered in Rwanda, and possibly its inclusion on the checklist of nationally legally protected species is recommendable.

Conflict of Interests

The author(s) have not declared any conflict of interests.

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REFERENCES

- Antonovics J, Hood ME, Thrall PH, Abrams JY, Duthie GM (2003). Herbarium studies on the distribution of anther-smut fungus (*Microbotryum violaceum*) and *Silene* species (Caryophyllaceae) in the eastern United States. *Am. J. Bot.* 90: 1522-1531. <http://dx.doi.org/10.3732/ajb.90.10.1522>; PMID:21659105.
- Ayalew A (2003). A floristic composition and structural analysis of Denkoro forest, South Wello. Master's Thesis, Addis Ababa University.
- Babaasa D, Bitariho R, Kasangaki A (2009). Some observations of the impact of *Sericostachys scandens* on forest regeneration in Bwindi Impenetrable Forest (Uganda). In: Chao N, Rugyerinyange L, and Scholte P (eds.). Conference on the Impact of *Sericostachys scandens* on the Conservation of Nyungwe National Park. Rwanda Environment Management, Kigali.
- Babaasa D, Eilu G, Kasangaki A, Bitariho R, McNeilage A (2004). Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *Afr. J. Ecol.* 42: 217-224. <http://dx.doi.org/10.1111/j.1365-2028.2004.00519.x>
- Bloesch U, Troupin G, Derungs N (2009). Les plantes ligneuses du Rwanda: Flore, ecologie et usages. Shaker Verlag, Aachen.
- Botanical Garden Meise (2014). The BR herbarium catalogue: *Hagenia abyssinica*. Available at: www.br.fgov.be (Last accessed on 23.02.2014).
- Chapman CA, Chapman LJ, Kaufman L, Zanne, AE (1999). Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. *Afr. J. Ecol.* 37: 81-92. <http://dx.doi.org/10.1046/j.1365-2028.1999.00159.x>
- Cowlishaw G, Dunbar R (2000). Primate conservation biology. University of Chicago Press, Chicago. PMID:11075706; PMCID:PMC1690772.
- DFGFI (2011). Notes from the field: Titus group sleeps outside of park again [Tuesday, November 8th, 2011]. Available at: www.gorillafund.org (Last accessed on 22.11.2011).
- Dondeyne S (1992). A study of the soils and vegetation of the Bisoke volcano (Rwanda). Report prepared for The Digit Fund, Katholieke Universiteit Leuven, Leuven.
- Dondeyne S, Deckers JA, Chapelle J (1993). The soils and vegetation of the Bisoke volcano (Rwanda): Habitat of mountain gorillas. *Pedol.* XLIII, 301-322.
- Eilu G, Hafashimana DLN, and Kasenene JM (2004). Tree species distribution in forests of the Albertine Rift, western Uganda. *Afr. J. Ecol.* 42: 100-110. <http://dx.doi.org/10.1111/j.1365-2028.2004.00504.x>
- Eilu G, Obua J (2005). Tree condition and natural regeneration in disturbed sites of Bwindi Impenetrable Forest National Park, southwestern Uganda. *Trop. Ecol.* 46: 99-111.
- FDRE (1994). Forestry Proclamation (NO. 94/1994). Federal Democratic Republic of Ethiopia, Addis Ababa.
- Feyissa T, Nybom H, Bartish IV, Welander M (2007a). Analysis of genetic diversity in the endangered tropical tree species *Hagenia abyssinica* using ISSR markers. *Genet. Resour. Crop. Evol.* 54: 947-958. <http://dx.doi.org/10.1007/s10722-006-9155-8>
- Feyissa T, Welander M, Negash L (2005). *In vitro* regeneration of *Hagenia abyssinica* (Bruce) J.F. Gmel. (Rosaceae) from leaf explants. *Plant Cell Rep.* 24: 392-400. <http://dx.doi.org/10.1007/s00299-005-0949-5>; PMID:15827747.
- Feyissa T, Zhu LH, Negash L, Welander M (2007b). Regeneration and genetic transformation of *Hagenia abyssinica* (Bruce) J.F. Gmel. (Rosaceae) with rolB gene. *Plant Cell Tissue Organ Cult.* 88: 277-288. <http://dx.doi.org/10.1007/s11240-006-9200-5>
- Fischer E, Killmann D (2008). Plants of Nyungwe National Park, Rwanda. Koblenz Geographical Colloquia, First Edition, Koblenz.
- Fuentes N, Pauchard A, Sanchez P, Esquivel J, Marticorena A (2013). A new comprehensive database of alien plant species in Chile based on herbarium records. *Biol. Invasions* 15: 847-858. <http://dx.doi.org/10.1007/s10530-012-0334-6>
- Gray M, McNeilage A, Fawcett K, Robbins M, Ssebide B, Mbula D, Uwingeli P (2005). Virunga volcanoes range mountain gorilla census, 2003.
- IUCN (2013). IUCN Red List of Threatened Species. Available at: www.iucnredlist.org (Last accessed on 24.02.2014).
- Kayijamahe E (2008). Spatial modelling of mountain gorilla (*Gorilla beringei beringei*) habitat suitability and human impact. Master's Thesis, International Institute of Geo-Information Science and Earth Observation, Netherlands.
- Karamuka F (1993). Variation spatio-temporelles des activités chez un groupe de gorilles de montagne (*Gorilla beringei beringei*) du parc National des Volcans. BSc Thesis, National university of Rwanda.
- Karlowski U (2006). Afromontane old-field vegetation: secondary succession and the return of indigenous species. *Afr. J. Ecol.* 44: 264-272. <http://dx.doi.org/10.1111/j.1365-2028.2006.00647.x>
- Kew Gardens (2014). Species browser: *Hagenia abyssinica* (*hagenia*). Available at: www.kew.org (Last accessed on 20.02.2014).
- Kibebew F, Addis G (1996). Utilization and conservation of medicinal plants in Ethiopia. Proceedings of the Workshop on Development Utilization of Herbal Remedies in Ethiopia.
- Lange S, Bussmann RW, Beck E (1997). Stand structure and regeneration of the subalpine *Hagenia abyssinica* forests of Mt. Kenya. *Bot. Acta* 110: 473-480. <http://dx.doi.org/10.1111/j.1438-8677.1997.tb00665.x>
- Leju JB (2004). Ecological recovery of an afromontane forest in southwestern Uganda. *Afr. J. Ecol.* 42: 64-69. <http://dx.doi.org/10.1111/j.1365-2028.2004.00463.x>
- Leju JB, Oryem-Origa H, Kasenene JM (2001). Regeneration of indigenous trees in Mgahinga Gorilla National Park, Uganda. *Afr. J. Ecol.* 39: 65-73. <http://dx.doi.org/10.1046/j.1365-2028.2001.00273.x>; <http://dx.doi.org/10.1111/j.1365-2028.2001.00273.x>
- McNeilage A (2001). Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins M, Sicotte P, Stewart KJ (Eds.). Mountain gorillas: three decades of research at Karisoke, Cambridge University Press, Cambridge. <http://dx.doi.org/10.1017/CBO9780511661631.011>; PMID:11367776
- McNeilage A (1995). Carte de la végétation du Parc National des Volcans.
- Milner JM, Harris S (1999). Habitat use and ranging behaviour of tree hyrax, *Dendrohyrax arboreus*, in the Virunga Volcanoes, Rwanda. *Afr. J. Ecol.* 37: 281-294. <http://dx.doi.org/10.1046/j.1365-2028.1999.00184.x>; <http://dx.doi.org/10.1046/j.1365-2028.1999.00185.x>
- Murererehe S (2000). Collecte et analyse de données pour l'aménagement durable des forêts -joindre les efforts nationaux et internationaux; Etat des ressources forestières au Rwanda. Technical Report, FAO, Rome.
- Norghauer JM, Nock CA, Grogan J (2011). The importance of tree size and fecundity for wind dispersal of Big-Leaf Mahogany. *Plos One* 6(3): e17488. <http://dx.doi.org/10.1371/journal.pone.0017488>; PMID:21408184; PMCID:PMC3049789.
- Nsazurwimo A (2004). Etude analytique des communautés de Bambous à *Sinarundinaria alpina* en rapport avec leur milieu écologique (cas du Parc National des Volcans). Mémoire, Butare, Université Nationale du Rwanda.
- Owiunji I, Nkuutu D, Kujirakwinja D, Plumtre A, Nsanzurwimo A, Fawcett K, Gray M, McNeilage A (2004). The biodiversity of the virunga volcanoes. WCS, DFGFI, ICCN, ORTPN, UWA, IGCP, Kigali.

- Paul JR, Randle AM, Chapman CA, Chapman LJ (2004). Arrested succession in logging gaps: is tree seedling growth and survival limiting? *Afr. J. Ecol.* 42: 245-251. <http://dx.doi.org/10.1111/j.1365-2028.2004.00435.x>
- Plumptre AJ (1993). The effects of trampling damage by herbivores on the vegetation of the Parc National des Volcans, Rwanda. *Afr. J. Ecol.* 32: 115-129. <http://dx.doi.org/10.1111/j.1365-2028.1994.tb00563.x>
- Plumptre AJ, Davenport TRB, Behangana M, Kityo R, Eilu G, Ssegawa P, Ewango C, Meirte D, Kahindo C, Herremans M, Peterhans JK, Pilgrim JD, Wilson M, Languy M, Moyer D (2007). The biodiversity of the Albertine Rift. *Biol. Conserv.* 134: 178-194. <http://dx.doi.org/10.1016/j.biocon.2006.08.021>
- Primature (2008). Official Gazette of the Republic of Rwanda, JO N°22 OF 15/11/2008 Year 47 n° 22 15 November 2008. Office of the Prime Minister, Kigali.
- Sarmiento EE, Butynski TM, Kalina J (1996) Gorillas of Bwindi impenetrable forest and the Virunga volcanoes: Taxonomic implications of morphological and ecological differences. *Am. J. Primatol.* 40: 1-21. [http://dx.doi.org/10.1002/\(SICI\)1098-2345\(1996\)40:1<1::AID-AJP1>3.0.CO;2-1](http://dx.doi.org/10.1002/(SICI)1098-2345(1996)40:1<1::AID-AJP1>3.0.CO;2-1)
- Seburanga JL (2007). Study of forest regeneration in disturbed and undisturbed areas of Mt Muhabura hillsides. BSc. Thesis (draft), National University of Rwanda.
- Seufert V, Linden B, Fischer F (2009). Revealing secondary seed removers: Results from camera trapping. *Afr. J. Ecol.* 48: 914-922. <http://dx.doi.org/10.1111/j.1365-2028.2009.01192.x>
- Shanahan M, So S, Compton S, Corlett R (2001). Fig-eating by vertebrate frugivores: A global Review. *Biol. Rev.* 76: 529-572. <http://dx.doi.org/10.1017/S1464793101005760>; PMID:11762492.
- Steklis HD, Madry S, Steklis NG, Faust N (2005). GIS Applications for Gorilla Behavior and Habitat Analyses. Available at: www.esri.com (Last accessed on 20.02.2014).
- Topp-Jørgensen JE, Marshal AR, Brink H, Pedersen UB (2008). Quantifying the response of tree hyraxes (*Dendrohyrax validus*) to human disturbance in the Udzungwa Mountains, Tanzania. *Trop. Conserv. Sci.* 1: 63-74.
- Troupin G (1982). Flore des plantes ligneuses du Rwanda: *Hagenia abyssinica* (Bruce) J. F. Gmelin. IRST, Butare.
- Turner IM (2001). The ecology of trees in the tropical rain forest. Cambridge Tropical Biology Series, Cambridge University Press, Cambridge. <http://dx.doi.org/10.1017/CBO9780511542206>
- Vamosi JC, Vamosi SM (2005). Present day risk of extinction may exacerbate the lower species richness of dioecious clades. *Divers. Distrib.* 11: 25-32. <http://dx.doi.org/10.1111/j.1366-9516.2005.00119.x>
- Van Gils H, Kayijamahe E (2009). Sharing natural resources: mountain gorillas and people in the Parc National des Volcans, Rwanda. *Afr. J. Ecol.* 48: 621-627.
- Verdoodt E, Van Ranst, E (2003). Land Evaluation for agricultural Production in the Tropics: A large-scale land suitability classification for Rwanda. Laboratory of Soil Science, Ghent University.
- Watts D (1983). Foraging strategy and sociology of mountain gorilla (*Gorilla gorilla beringei*) and their relation to food availability. University of Chicago.
- Weber W, Vedder AL (1983). Population dynamics of the virunga gorillas: 1959-1978. *Biol. Conserv.* 26: 341-366. [http://dx.doi.org/10.1016/0006-3207\(83\)90096-4](http://dx.doi.org/10.1016/0006-3207(83)90096-4)
- White L, Edwards A (2000). Conservation en forêt pluviale africaine: Méthodes de recherche. Wildlife Conservation Society, New York.