Selective logging: Do rates of forest turnover in stems, species composition and functional traits decrease with time since disturbance? – A 45 year perspective

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ABSTRACT

Selective logging, the targeted harvesting of timber trees in a single cutting cycle, is globally rising in extent and intensity. Short-term impacts of selective logging on tropical forests have been widely investigated, but long-term effects on temporal dynamics of forest structure and composition are largely unknown. Understanding these long-term dynamics will help determine whether tropical forests are resilient to selective logging and inform choices between competing demands of anthropogenic use versus conservation of tropical forests. Forest dynamics can be studied within the framework of succession theory, which predicts that temporal turnover rates should decline with time since disturbance. Here, we investigated the temporal dynamics of a tropical forest in Kibale National Park, Uganda over 45 years following selective logging. We estimated turnover rates in stems, species composition, and functional traits (wood density and diameter at breast height), using observations from four censuses in 1989, 1999, 2006, and 2013, of stems ⩾10 cm diameter within 17 unlogged and 9 logged 200 × 10 m vegetation plots. We used null models to account for interdependencies among turnover rates in stems, species composition, and functional traits. We tested predictions that turnover rates should be higher and decrease with increasing time since the selective logging event in logged forest, but should be less temporally variable in unlogged forest. Overall, we found higher turnover rates in logged forest for all three attributes, but turnover rates did not decline through time in logged forest and was not less temporally variable in unlogged forest. These results indicate that successional models that assume recovery to pre-disturbance conditions are inadequate for predicting the effects of selective logging on the dynamics of the tropical forest in Kibale. Selective logging resulted in persistently higher turnover rates, which may compromise the carbon storage capacity of Kibale's forest. Selective logging effects may also interact with effects from other global trends, potentially causing major long-term shifts in the dynamics of tropical forests. Similar studies in tropical forests elsewhere will help determine the generality of these conclusions. Ultimately, the view that selective logging is a benign approach to the management of tropical forests should be reconsidered in the light of studies of the effects of this practice on long-term forest dynamics.

1. Introduction

Selective logging, the targeted harvesting of timber trees in a single cutting cycle, is rising in extent and intensity on a global scale likely due to its increasing importance as a source of revenue for developing economies (Asner et al., 2009). Conservative estimates that do not account for clandestine (but presumably prevalent) logging operations indicate that at least 390 million hectares of tropical humid forests were selectively logged as of 2009 (Asner et al., 2009). In 2011, 403 million hectares of tropical forest were officially reserved for timber production (Putz et al., 2012). These figures have prompted the question of whether selective logging has transitioned from a relatively benign land-use practice to a significant threat to the conservation value of tropical forests (Asner

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et al., 2009). Consequently, there is growing interest in understanding the impacts of selective logging on tropical forests, including not only immediate consequences for forest structure and composition, but also effects on long-term compositional and structural dynamics (Anderson-Teixeira et al., 2013; Sist et al., 2015).

While the short-term impacts of selective logging on the state of tropical forests have been widely investigated (Cannon et al., 1998; Bonnell et al., 2011; Gibson et al., 2011; Baraloto et al., 2012; Putz et al., 2012), the long-term effects of selective logging on temporal dynamics of forest structure and composition are largely unknown. These dynamics can be studied within the framework of succession, the temporal change in structure or composition of a group of species co-occurring at a site (Pickett et al., 2011; Prach and Walker, 2011). A key feature of successional trajectories, central to our understanding of the dynamics of species assemblages, is variation in the rates of temporal change in structure and composition. These rates often referred to as "temporal turnover rates" describe temporal changes in recruitment and mortality of individuals (a.k.a stem turnover *sensu* Lewis et al., 2004b), species composition or functional traits. Functional traits are morphological and physiological traits that reflect allocation strategies thought to be important determinants of fitness across environments (Violle et al., 2007). Turnover rates are expected to decrease as succession ensues (Drury and Nisbet, 1973; Whittaker, 1975; Grime, 1979; Bornkamm, 1981; Anderson, 2007), presumably due to replacement of pioneers at early stages of succession by longer-lived, self-replacing, late-successional species, and a higher resistance to invasion resulting in fewer species being added at later stages of succession (Facelli and Angela, 1990; Myster and Pickett, 1994; Anderson, 2007; Walker and del Moral, 2008). Declining rates of temporal turnover as succession proceeds have been consistently documented across a wide range of species assemblages, including phytoplankton communities (Jassby and Goldman, 1974), herbaceous and shrub plant communities (Bornkamm, 1981; Prach et al., 1993; Myster and Pickett, 1994; Anderson, 2007; Matthews and Endress, 2010), forest tree communities (Anderson, 2007), and aquatic communities including zooplankton, benthic macroinvertebrates, and fish (Korhonen et al., 2010).

Chronosequence approaches have shown that stem turnover rates decline with successional stage post logging in a tropical forest (Sheil et al., 2000). However, because long-term data on temporal change of tree communities are difficult to obtain, only a few studies have used temporal data to investigate the effect of selective logging on the successional trajectories of tropical forests. Of these, most have focused on temporal variation in stem density (Verburg and van Eijk-Bos, 2003), recruitment and mortality rates (Sheil et al., 2000; Chapman and Chapman, 2004; Bonnell et al., 2011), and aboveground biomass and carbon stocks (Blanc et al., 2009; Gourlet-Fleury et al., 2013). Studies focused on species composition have mainly used ordination methods to establish the direction of temporal change and determine whether selectively logged forests converge on a steady-state through time (Verburg and van Eijk-Bos, 2003). For functional traits, Sheil et al. (2000) used taxon analysis to test whether the proportion of shade tolerant trees changes as succession progresses after selective logging, while Carreño-Rocabado et al. (2012) evaluated changes in the functional diversity of tropical tree communities from 12 traits and the underlying role of demographic processes, over two time points that spanned 8 years following selective logging. To date, no studies have explicitly used long-term data to test the expectation that turnover rates decrease as succession proceeds following selective logging.

To the best of our knowledge, there are no studies that simultaneously examine the effect of selective logging on temporal turnover rates in stems, species composition and functional traits. Yet, doing so is important for at least two reasons. One is that predictions of succession theory might be supported for only some of these three kinds of turnover rate. Temporal turnover rates in stems and functional traits are expected to show systematic trends as succession proceeds, due to replacement of pioneers with longer-lived species (Bazzaz and Pickett, 1980; Bazzaz, 1996; Walker and del Moral, 2008), and because environmental filters are thought to act on traits that determine dispersal, survival, and reproduction in different environments (Shipley, 2010). However, temporal turnover rates in species composition might not show systematic trends if several species have similar functional traits and species occurrences are historically contingent on stochastic factors, such as which species arrive first at a site (Fukami et al., 2005; Shipley, 2010). Thus, temporal turnover rates in stems and functional attributes during forest succession might be more predictable than temporal turnover rates in species composition (Guariguata and Ostertag, 2001; Chazdon et al., 2007). It follows that support for the prediction of decreasing turnover rates as succession proceeds may depend on whether turnover rate is measured in terms of stems, species composition, or functional traits (Anderson, 2007).

A second reason to simultaneously study turnover rates in stems, species composition, and functional traits is that it allows controlling for dependencies among these three kinds of turnover rate and, thus, understanding the extent to which each kind of turnover rate behaves independently as predicted by succession theory. For instance, turnover rates in species composition and functional traits depend at least in part on turnover rate in stems. At one extreme, if the stem turnover rate is zero (i.e. stems neither die nor recruit), then turnover rate in species composition and functional traits are bound to be zero as well. As stem turnover rate increases it is possible for turnover in species composition and functional traits to increase, but only within the limits imposed by stem turnover rate. For example, the number of new species entering a site during a given time interval cannot possibly exceed the number of stems recruited in that site. Likewise, the number of species lost from a site during a given time interval cannot possibly exceed the number of stems dying in that site. In analogous fashion, turnover rate in species composition limits turnover rate in functional traits (Swenson et al., 2012). Thus, when testing if turnover rate in species composition decreases in a decelerating manner while succession occurs, as predicted by succession theory, it is desirable to control for stem turnover rate. Likewise, when testing if turnover rate in functional traits decreases in a decelerating manner as succession proceeds, it is useful to control for turnover rate in stems and species composition. We are unaware of studies of the effect of selective logging on temporal turnover rates that implement these kinds of control.

Here, we investigated the temporal dynamics of a tropical forest in Kibale National Park, Uganda during 45 years following selective logging. Given the predictions of succession theory, we tested the working hypothesis that turnover rates in stems, species composition and functional traits decline in selectively logged forest but not in unlogged forest. This working hypothesis is reasonable because declining turnover rates characterize successional trajectories in many systems (see above). In particular, we examined three predictions about turnover rates derived from the working hypothesis (Fig. 1). First, during the first several years after a selective logging event, turnover rates should be higher in logged than in unlogged forest. This first prediction follows from the idea that the selectively logged forests are reset to a relatively earlier stage of succession due to the removal and damage of biomass. The time interval to which this prediction applies depends on the rate of replacement of early successional species by late successional species. In tropical forests, this replacement may take decades
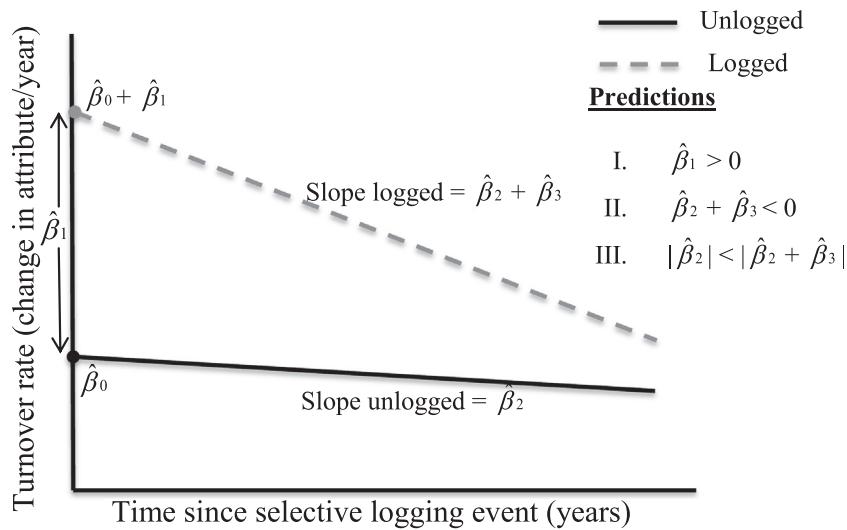
Fig. 1. Conceptual figure illustrating predictions based on succession theory. Predictions are expressed in a linear regression framework, focusing on the intercepts and slopes. $\hat{\beta}_0$ is the intercept (i.e. turnover rate when time since selective logging event equals zero) for unlogged plots, $\hat{\beta}_1$ is the difference in intercepts between unlogged and logged plots, such that the intercept for logged plots equals $\hat{\beta}_0 + \hat{\beta}_1$. $\hat{\beta}_2$ is the slope for the effect of time on turnover rates in unlogged plots. $\hat{\beta}_3$ is the difference in slopes between logged and unlogged plots, such that the slope for logged plots equals $\hat{\beta}_2 + \hat{\beta}_3$. Prediction I: higher turnover rates in logged plots, implies $\hat{\beta}_1 > 0$. Prediction II: declining temporal turnover rates in logged plots, implies $\hat{\beta}_2 + \hat{\beta}_3 < 0$. Prediction III: less temporally variable turnover rates in unlogged plots, implies $|\hat{\beta}_2| < |\hat{\beta}_2 + \hat{\beta}_3|$.

(Guariguata and Ostertag, 2001; Lebrija-Trejos et al., 2010). Second, turnover rates in selectively logged forests should decrease with increasing time since the selective logging event, which indicates that forest stability is increasing as succession ensues. Third, turnover rates in unlogged forest should be less temporally variable than in selectively logged forests. Beyond testing these predictions with raw observed turnover rates in stems, species composition and functional traits, we also conducted tests based on null models that account for dependencies among these three kinds of turnover rate. Specifically, we used null models based on random sampling from a regional species pool (Gotelli and McGill, 2006) to account for (i) the turnover rate in species composition expected by chance from the observed turnover rate in stems, (ii) the turnover rate in functional traits expected by chance from the observed turnover rate in stems, and (iii) the turnover rate in functional traits expected by chance from the observed turnover rate in species composition.

2. Materials and methods

2.1. Study site

This study was conducted in Kibale National Park (here-after Kibale), South-western Uganda, which covers 795 km^2 in area (Chapman et al., 2010). It is predominantly mature moist semi-deciduous and ever-green forest, but includes a variety of other habitats including grassland, woodland, lakes and wetlands, secondary forest, and regrowth in areas previously planted with exotic trees (Chapman and Lambert, 2000). Kibale receives an average rainfall of 1643 mm annually (1990–2013; Chapman and Chapman unpublished data collected at Makerere University Biological Field Station) with two peak rainy seasons from March to May and September to November (Chapman et al., 2010). Temperature ranges between an average daily minimum of 15.5 °C and daily maximum of 23.7 °C. Kibale is divided into compartments which were subjected to varying degrees of logging, and have experienced different restoration efforts (Struhsaker, 1997; Chapman et al., 2010). Our study involved three compartments within Kibale (Fig. 2). The first, K-30 (282 ha), has a recent history that is relatively free of human disturbance, and is typically considered a mature old-growth forest. The second, K-14 (405 ha), was selectively logged between May and December 1969 in a spatially heterogeneous manner, so that some areas (Mikana) experienced heavy logging with the removal and damage of up to 25% of all trees, while other areas were largely untouched. The third, K-15 (347 ha), experienced high intensity selective logging between September 1968 and April 1969 resulting in removal and damage of up to 50% of all trees.

2.2. Vegetation plots

Twenty-six permanent vegetation plots were randomly established within the existing trail system in Kibale in December 1989. Each plot is 200 × 10 m with the shorter plot dimension bisected by a trail. These plots were originally established with the purpose of long-term monitoring of tree phenology (Chapman et al., 2010). The locations of the 26 plots were unevenly distributed across the three compartments; 11 plots were located in K-30, six were in the lightly logged, and four in the heavily logged (Mikana) parts of K-14, and five were in K-15. We assigned each vegetation plot to one of two categories according to disturbance history: unlogged or selectively logged. We placed the 17 plots in K-30 and the lightly logged areas of K-14 in the unlogged category, and the 9 plots in the Mikana part of K-14 and in K-15 in the selectively logged category. The assignment of plots in the largely untouched areas of K-14 to the unlogged category was informed by earlier work showing that these areas suffered little if any damage from the logging event based on stump and gap enumeration (Kasenene, 1987; Chapman and Chapman, 1997; Bonnell et al., 2011).

2.3. Data collection

2.3.1. Censuses of vegetation plots

The 26 plots have been censused between March and May at four time points: 1989, 1999, 2006, and 2013. Hereafter we refer to these censuses as C_1, C_2, C_3 and C_4 respectively. Censuses of each plot involved following the fate of all trees with diameter at breast height (DBH) $\geqslant$ 10 cm, including recruitment of new stems and mortality of existing stems (Chapman et al., 2010). Trees were

Fig. 2. Location of study site in Kibale National Park (Kibale), southwest Uganda, East Africa. Left panel shows the location of 26 vegetation plots, northwest of Kibale. Right panel shows the detailed spatial arrangement of logged ($N = 9$) and unlogged ($N = 17$) vegetation plots within Kibale.

determined to species using taxonomic keys (Polhill, 1952; Hamilton, 1991; Katende et al., 1995; Lwanga, 1996), and species names updated using The Plant List (http://www.theplantlist.org/). The census dataset provides information on stem number, species composition, and species abundances for each plot at four time points.

2.3.2. Functional traits

We focused on two functional traits thought to be important in successional forest dynamics: Wood density (WD; g/cm^3) and maximum diameter at breast height (DBH$_{MAX}$; cm). Maximum diameter at breast height provides a measure of potential adult stature, which is a crucial component of a species light competitive ability and carbon gain strategy (King et al., 2006). Both WD and adult stature are thought to vary with species' light requirements and forest successional stage (Falster and Westoby, 2005; Chave et al., 2009). To estimate DBH$_{MAX}$ we measured DBH as the circumference of a tree trunk at 1.2 m height for all stems in the 26 plots during C_1, C_2, C_3, and C_4. Species DBH$_{MAX}$ was considered the largest DBH value recorded for all individuals of a species from all 26 plots across all four censuses. DBH data were available for all 91 species that occurred in the plots across all censuses.

Wood density, a measure of a tree's dry carbon investment per unit volume, is considered a key indicator of the wood economic spectrum due to its strong connection with several aspects of a plant's ecology including growth rate, carbon allocation strategy, structural stability, hydraulic conductivity, and disease or pest resistance (Chave et al., 2009). To measure WD, we randomly selected ten plots (five in the unlogged and five in selectively logged forest) and extracted wood cores with an increment borer from 687 upright adult trees. Details of sampling and method for wood density determination are described in Osazuwa-Peters et al. (2015). From the ten sampled plots, we could determine

species mean WD for 61 species out of the 91 species found across all 26 plots and censuses. For the remaining 30 species, we obtained species, genus, or family level WD means from the Global Wood Density Database subset for African region (Zanne et al., 2009) with as fine a taxonomic resolution as was available in the database. There were WD values for 7 of the missing species, genus-level WD values for 11 species, and family-level WD values for the remaining 12 species. Consequently, we had two WD datasets for Kibale's species; one incomplete dataset composed of WD values measured directly and a second complete dataset that included data compiled from the Global Wood Density Database. These two datasets were used to perform two versions of all analyses involving functional traits. However, we only discuss the results based on the incomplete dataset when they differ from those based on the complete dataset (see below).

2.4. Forest turnover rates

We quantified turnover rates in stems, species composition, and functional traits, over three census intervals, between consecutive pairs of censuses (C_1–C_2, C_2–C_3, C_3–C_4). The census intervals varied in length; the first census interval was 10 years, and the second and third census intervals were 7 years. Theoretical (Sheil and May, 1996) and empirical (Lewis et al., 2004b) work indicates that, in the presence of variation of census intervals and heterogeneity in turnover rates within a forest stand at a particular point in time, turnover rate estimates are affected by a potentially serious artifact. In particular, turnover rate estimates are negatively related to the census interval on which they are based. In this study, such artifact may be problematic for testing the second prediction derived from the working hypothesis, which states that turnover rates decline through time. To address this potential artifact, we applied the generic correction factor developed by Lewis et al.

(2004b) to all estimates of turnover rates. This correction involves standardizing turnover rate estimates to a common census length using $\lambda_{corr} = \lambda \times t^{0.08}$, where λ is the turnover rate and t is time between censuses in years. This correction had only minor effect on details of the results, and no effect on conclusions reached regarding tests of different predictions derived from the working hypothesis. Therefore, for simplicity, we present in the main text the results for uncorrected turnover rates, and place the results based on corrected turnover rates in supplementary material (Appendices E.1 and E.2).

2.4.1. Stem turnover rate

Turnover rate in stems (T_S) in a given plot was defined as the average of the number of stems gained (recruited) and lost (dead, missing, or broken) between two consecutive censuses, weighted by the average number of stems in the two censuses and the time interval (t) between the two censuses (Anderson, 2007):

$$T_S = \frac{\frac{1}{2}\left(\frac{D+R}{t}\right)}{\frac{1}{2}\left[SN_{Cj} + SN_{Cj+1}\right]} \tag{1}$$

where D is number of dead, missing, or broken stems in a plot between two consecutive censuses; R is number of recruited stems between two consecutive censuses; SN_{Cj} is total number of stems counted in the census C_j; and j takes the values 1–3 (see above section on censuses of vegetation plots).

2.4.2. Species composition turnover rate

Rate of turnover in species composition (T_{SC}) was defined as the change in species composition in a plot between two consecutive censuses (t), weighted by the time interval between the two censuses. We measured this rate using raw metrics of dissimilarity in species composition, as well as metrics based on a null model that accounted for stem turnover rate.

We used two raw metrics of dissimilarity in species composition. The first was Bray–Curtis index (Bray and Curtis, 1957):

$$T_{SCBRAY_{Cj,Cj+1}} = \frac{\sum_i |x_{iCj+1} - x_{iCj}| / \sum_i |x_{iCj} + x_{iCj+1}|}{t} \tag{2}$$

where x_{iCj} is abundance of species i in a given plot at census C_j. The second raw metric was the β component of the Rao's index for taxonomic diversity (Rao, 1982; De Bello et al., 2010):

$$T_{SCRAO_{Cj,Cj+1}} = \frac{100 * (\gamma\, Rao - \bar{\alpha}\, Rao)/\gamma\, Rao}{t} \tag{3}$$

where $\gamma\, Rao$ is total diversity obtained by pooling data from two consecutive censuses of a plot (C_j and C_{j+1}), and $\bar{\alpha}\, Rao$ is the average of two $\alpha\, Rao$ values, each representing diversity during one of two consecutive censuses of a plot. Both $\gamma\, Rao$ and $\alpha\, Rao$ are sums of the products of the relative abundances of all possible pairs of species. However, the relative abundance of each species is calculated as an average across two consecutive censuses in the case of $\gamma\, Rao$, while in the case of $\alpha\, Rao$ only data from a single census is considered (Rao, 1982; De Bello et al., 2010).

Raw metrics of turnover rate in species composition, such as $T_{SC.BRAY}$ and $T_{SC.RAO}$, depend at least in part on turnover rates in stems (see Section 1). It follows that differences between logged and unlogged forests in raw metrics of turnover rates in species composition may be due partially or entirely to stem turnover rates. Thus, we tested the predictions about turnover rates in species composition using a null model that accounts for the effect of observed stem turnover rate on species composition turnover rate, assuming random sampling from a regional species pool (Gotelli and McGill, 2006). This null model preserved observed mortality and recruitment rates, as well as observed number of stems in each plot at each census. However, the individual stems that died in a

plot during any given time interval, were randomly chosen from the stems found in the plot at the beginning of the time interval. Recruitment was simulated by randomly sampling individuals from a regional species abundance distribution that included all species found in the 26 plots during all censuses. The abundance of each species in this distribution was defined as the average abundance for that species over the four censuses (following Gotelli et al., 2010). We performed 1000 iterations of the null model for each plot at each census interval (C_1–C_2, C_2–C_3, and C_3–C_4), generating 1000 null turnover values per plot and census interval. Using this null model we computed turnover rate in species composition as the standardized effect size (SES): the difference between observed turnover and expected turnover under the null model (i.e., the mean of 1000 turnover values generated by the null model) divided by the standard deviation of turnover values generated by the null model. We estimated two SES metrics of turnover rate in species composition based on the two raw metrics: Bray–Curtis ($T_{SCBRAY.SES1}$) and Rao's index ($T_{SCRAO.SES1}$).

2.4.3. Functional trait turnover rate

Rate of turnover in functional traits (T_{FC}) was defined as the change in functional trait composition within a plot between two consecutive censuses, weighted by the time interval (t) between the two censuses (t). We measured rate of turnover in functional traits using raw metrics of dissimilarity in functional traits, as well as metrics based on null models that accounted for turnover rates in stem number and species composition.

We used two raw metrics of turnover in functional traits. The first was absolute difference in community weighted mean between two consecutive censuses:

$$T_{|\Delta CWM|trait_{Cj,Cj+1}} = \frac{|CWM_{Cj+1} - CWM_{Cj}|}{t}, \tag{4}$$

where CWM_{Cj} is the inter-specific mean of a trait value, weighted by the relative abundance of each species at census C_j. We calculated this metric to measure turnover rate in each of the two functional traits, WD or DBH$_{MAX}$, and refer to the respective measures as $T_{|\Delta CWM|WD}$ and $T_{|\Delta CWM|DBHMAX}$.

The second raw metric of turnover in functional traits was the β component of Rao's index for functional diversity (T_{FCRAO}) in the Euclidean space defined by the two functional traits, WD or DBH$_{MAX}$:

$$T_{FCRAO_{Cj,Cj+1}} = \frac{100 * (\gamma_{FD}\, Rao - \bar{\alpha}_{FD}\, Rao)/\gamma_{FD}\, Rao}{t}, \tag{5}$$

where $\gamma_{FD}\, Rao$ is functional diversity obtained by pooling data from two consecutive censuses of a plot (C_j and C_{j+1}), and $\bar{\alpha}_{FD}\, Rao$ is the average of two $\alpha_{FD}\, Rao$ values, each representing functional diversity during one of two consecutive censuses of a plot. Both $\gamma_{FD}\, Rao$ and $\alpha_{FD}\, Rao$ are sums of the Euclidian distances between all possible pairs of species in space defined by the two functional traits weighted by the product of the relative abundances of the respective species pairs. However, the relative abundance of each species is calculated as an average across two consecutive censuses in the case of $\gamma_{FD}\, Rao$, while in the case of $\alpha_{FD}\, Rao$ only data from a single census is considered.

Raw metrics of turnover rate in functional traits depend at least partly on turnover rates in stems and species composition (see Section 1). Therefore, we used two null models to account for the effect of turnover rates in stems and species composition on turnover rate in functional traits. The first null model, hereafter null model 1, is identical to the null model described in the section on species composition turnover rates (above). It accounts for the effect of turnover rates in stems on turnover rate in functional traits, assuming sampling from a regional species pool. The second null model, hereafter null model 2, randomized trait values among

species before the first census interval, while maintaining the observed species abundance, species richness, and species turnover through time. Null model 2 yielded expected values of turnover rate in functional traits for observed values of species turnover in a plot, assuming trait values were randomly sampled from the set of observed trait values among all species found in the 26 plots during all censuses. In this null model, combinations of values for the two functional traits (WD and DBH_{MAX}) were not altered, but kept fixed so as to preserve observed interspecific correlations among traits (Schleicher et al., 2011). We conducted 1000 iterations of each null model for each plot and census interval, and calculated standardized effect sizes (*SES*, described above) for each of the raw metrics of turnover rates in functional traits. Extending the abbreviations for these raw metrics, we refer to *SES* values obtained from null model 1 as $T_{|\Delta CWM|WD.SES1}$, $T_{|\Delta CWM|DBHMAX.SES1}$, and $T_{FCRAO.SES1}$. Likewise, we refer to *SES* values obtained from null model 2 as $T_{|\Delta CWM|WD.SES2}$, $T_{|\Delta CWM|DBHMAX.SES2}$, and $T_{FCRAO.SES2}$.

2.5. Statistical tests of predictions

We evaluated the three predictions described in Section 1 for 14 turnover rate metrics (defined above): T_S, T_{SCBRAY}, T_{SCRAO}, $T_{|\Delta CWM|WD}$, $T_{|\Delta CWM|DBHMAX}$, T_{FCRAO}, $T_{SCBRAY.SES1}$, $T_{SCRAO.SES1}$, $T_{|\Delta CWM|WD.SES1}$, $T_{|\Delta CWM|DBHMAX.SES1}$, $T_{FCRAO.SES1}$, $T_{|\Delta CWM|WD.SES2}$, $T_{|\Delta CWM|DBHMAX.SES2}$, and $T_{FCRAO.SES2}$. To gauge empirical support for these predictions, we used linear mixed effects models (lme) with restricted maximum likelihood ratio method (Bolker et al., 2009). These lme models allowed us to express the three predictions of interest in terms of fixed effects, while simultaneously modeling the variance among plots as a random effect. The general structure for the lme models we used was as follows:

$$TR_{iC_j} = (\beta_0 + U_{0,i}) + (\beta_1) \cdot Lo_i + (\beta_2 + U_{2,i}) \cdot Time_{iC_j} + (\beta_3) \cdot Lo_i \cdot Time_{iC_j} + \varepsilon_{iC_j}, \qquad (6)$$

where TR_{iC_j} is turnover rate (as estimated by any of the 17 metrics above) in plot i ($i = 1, \ldots, 26$) measured at census C_j ($j = 2, 3,$ or 4), Lo_i is a dummy variable denoting whether plot i belongs to the unlogged ($Lo_i = 0$) or logged ($Lo_i = 1$) category, and $Time_{iC_j}$ is the number of years elapsed since the selective logging event when turnover was measured in plot i at census C_j ($Time_{iC_j} = 31, 38$ or 45 years). $Time_{iC_j}$ was rescaled by subtracting the length of time that had elapsed since the logging event at census C_2 (31 years). Given this rescaling, the model intercept equals the first turnover rate that we measured. In particular, the first coefficient in Eq. (6), β_0, represents the average intercept for plots in the unlogged category. In other words, β_0 is the average (across plots in the unlogged category) annualized turnover rate during the first census interval 31 years after the selective logging event. Coefficient β_1 is the difference in average intercept between plots in the logged and unlogged categories. The sum of the first two terms in Eq. (6), $\beta_0 + U_{0,i}$, is the intercept for plot i in the unlogged category. Likewise, the sum of the first three terms, $\beta_0 + U_{0,i} + \beta_1$, is the intercept for plot i in the logged category. So $U_{0,i}$ is the extent to which the intercept of plot i deviates from the average intercept for the respective category (unlogged or logged). Coefficient β_2 is the average slope relating turnover rate to time since the selective logging event for plots in the unlogged category. Coefficient β_3 is the difference in this slope between the logged and unlogged categories. The value of $U_{2,i}$ is the extent to which the slope of plot i deviates from the average slope for the respective category (unlogged or logged). Finally, ε_{iCj} represents the difference between predicted and observed turnover rate in plot i at census C_j. Terms $U_{0,i}$, $U_{2,I}$, and ε_{iCj} are random effects, while all other coefficients in Eq. (6) are fixed effects. Further details of model specification are described in Appendices A and B.

Now we can express the three predictions described in Section 1 in terms of coefficients in the general model represented in Eq. (6). From here on, these coefficients are indicated with carets to denote that they are sample-based estimates of population parameters. The first prediction is that during several years after a selective logging event, turnover rate should be higher in selectively logged forest than in unlogged forest. Based on previous studies (see Section 1 and the Methods section on censuses of vegetation plots) we assumed that this prediction still applies 31 years after the selective logging event. Thus, in terms of Eq. (6) the first prediction can be expressed as: $\hat{\beta}_1 > 0$ (Fig. 1). The second prediction is that turnover rate in selectively logged forest should decrease with increasing time since the selective logging event. In terms of Eq. (6), this prediction can be expressed as: $\hat{\beta}_2 + \hat{\beta}_3 < 0$ (Fig. 1; Appendix C.1 for details). The last prediction is that turnover rate in unlogged forest should be less temporally variable than in selectively logged forest. In terms of Eq. (6) this prediction can be expressed as: $|\hat{\beta}_2| < |\hat{\beta}_2 + \hat{\beta}_3|$ (Fig. 1). To determine empirical support for this last prediction, it is necessary to consider the signs of $\hat{\beta}_2$ and $\hat{\beta}_3$. If $\hat{\beta}_3$ and $\hat{\beta}_2$ have the same sign, and $\hat{\beta}_3$ is statistically significant (i.e. it is different from zero), then the third prediction is supported. On the other hand, if $\hat{\beta}_3$ and $\hat{\beta}_2$ have different signs, the prediction is supported only if $|\hat{\beta}_3| - 2^* |\hat{\beta}_2| > 0$ (see Appendix C.2 for details).

Because logging happened in a spatially structured way across the study area in Kibale, plots in the logged category occurred in more northerly latitudes than those in the unlogged category (Fig. 2). Consequently, spatial processes could influence forest turnover rates independent of the effects of selective logging (Lindenmayer and Laurance, 2012; Ramage et al., 2013). To control for the potential effects of unmeasured factors that co-vary linearly with space, we added latitude of each plot as a variable in lme models. The lme models that included latitude had an additional coefficient, β_4, representing the average slope (across plots) of the relationship between turnover rate and latitude. Using spatial variables (e.g., latitude) in this fashion reduces Type I error (Peres-Neto and Legendre, 2010) and provides a more conservative test of the predictions of interest. We compared models that included latitude with those that did not using Akaike's Information Criterion corrected for finite sample sizes (AIC$_c$, Burnham and Anderson, 2002). We followed the general rule of thumb that $\Delta AIC_c \leqslant 2$ indicates similar empirical support (Appendix D). In all cases when multiple models had similar empirical support, there were no differences in the results of the test of the predictions. We present only one model for each metric of turnover rate even when multiple models have similar empirical support. Also, we examined model residuals to evaluate departure from assumptions of linearity, as well as variance homogeneity and normality of errors. To better approximate these assumptions we applied the logarithmic transformation to T_{SCRAO} and T_{FCRAO}, and the square root transformation to $T_{|\Delta CWM|DBHMAX}$.

All statistical tests were implemented in R version 2.15.1 (R Core Team, 2012). Packages used included *vegan* (Oksanen et al., 2012) for Bray–Curtis index, package *FD* (Laliberté and Legendre, 2010; Laliberte and Shipley, 2011) for community weighted means, and packages *cluster* (Maechler et al., 2012), *ade4* (Dray and Dufour, 2007) and a sourced script (rao_script.R) (De Bello et al., 2010) for Rao's index. The lme models were performed with the nlme package (Pinheiro et al., 2007), caterpillar plots obtained with lme4 package (Bates et al., 2013), and ΔAIC_c and AIC$_c$ weights obtained with the AICcmodavg package (Mazerolle, 2013).

3. Results

3.1. Stem turnover rate

In accord with the first prediction (Fig. 1), plots in the logged category had a higher intercept for stem turnover rate than plots in the unlogged category ($\hat{\beta}_1 > 0$, Table 1), indicating that stem turnover rate was higher in logged than unlogged forest 31 years after the selective logging event (Fig. 3A). However, contrary to the second prediction (Fig. 1), stem turnover rate for plots in the logged category did not change with time ($\hat{\beta}_2 + \hat{\beta}_3 = 0$, Table 1, Fig. 3A). Moreover, the third prediction (Fig. 1) was not supported because stem turnover rate was not less temporally variable for plots in the unlogged than in the logged category ($\hat{\beta}_3 < 2^* \hat{\beta}_2$, Table 1, Fig. 3A).

3.2. Species composition turnover rate

Estimates of turnover rate in species composition only partially supported the first prediction of higher intercept for plots in the logged than unlogged category. When measured with raw metrics of species turnover rate, plots in the logged category had higher intercepts than plots in the unlogged category ($\hat{\beta}_1 > 0$ if critical p-value = 0.1, Table 1, Fig. 3B and D). These results seemed to reflect the influence of stem turnover rate on species composition turnover rate (see Section 1). In particular, metrics of species composition turnover rate based on null models that control for stem turnover rate revealed either no difference in intercept between plots in the logged and unlogged categories, or lower intercept for plots in the logged category ($\hat{\beta}_1 \leqslant 0$, Table 1, Fig. 3C and E).

Estimates of turnover rate in species composition for plots in the logged category did not decrease through time ($\hat{\beta}_2 + \hat{\beta}_3 \geqslant 0$, Table 1, Fig. 3B–E) and, thus, did not support the second prediction. Indeed, as measured by two raw metrics, turnover rate in the species composition of plots in the logged category tended to increase through time, albeit for one of these metrics the increase was not significant (Table 1). This trend of temporal increase in turnover rates did not seem to result from the effect of stem turnover rate

on species composition turnover rate, because it persisted when species composition turnover rate was measured by metrics based on null models that control for stem turnover rate (Table 1).

The third prediction (Fig. 1) was only partially supported by estimates of turnover rate in species composition. Raw metrics of turnover rate in species composition provided no support for this prediction, because turnover rate was not less temporally variable for plots in the unlogged than in the logged category ($|\hat{\beta}_2| \geqslant |\hat{\beta}_2 + \hat{\beta}_3|$, Table 1, Fig. 3B and D). However, as measured by one of the metrics that accounts for stem turnover rate ($T_{SBRAY.SES1}$), turnover rate in species composition for plots in the unlogged category was marginally less temporally variable than that for plots in the logged category ($|\hat{\beta}_2| < |\hat{\beta}_2 + \hat{\beta}_3|$, if critical p-value = 0.1, Table 1, Fig. 3C).

3.3. Functional trait turnover rate

One out of nine metrics of turnover rate in functional traits ($Tfcrao$) supported the first prediction of higher intercept for the logged than unlogged category ($\hat{\beta}_1 > 0$, Table 1). However, this result seemed driven by the effect of stem turnover rate on functional trait turnover rate. The metric controlling for such an effect ($T_{FCRAO.SES1}$) did not support the first prediction ($\hat{\beta}_1 \leqslant 0$, Table 1). None of the other metrics of turnover rate in functional traits provided support for the first prediction (in all cases $\hat{\beta}_1 \leqslant 0$, Table 1, Fig. 3F–G).

We found no support for the second prediction, as none of the metrics of turnover rate in functional traits decreased through time for plots in the logged category (in all cases $\hat{\beta}_2 + \hat{\beta}_3 \geqslant 0$, Table 1, Fig. 3F–G). Similarly, we found no support for the third prediction, according to which turnover rate should be less temporally variable in unlogged than selectively logged forest (Fig. 1). As estimated by all nine metrics, turnover rate in functional traits was not less temporally variable for plots in the unlogged than for plots in the logged category (in all cases $|\hat{\beta}_2| \geqslant |\hat{\beta}_2 + \hat{\beta}_3|$, Table 1, Fig. 3F and G).

When the analyses were based on the incomplete functional trait dataset, there was no support for any of the three predictions,

Table 1

Empirical support for the three predictions derived from the working hypothesis that logged forest has undergone declining rates of turnover (Fig. 1). The two columns under prediction III correspond to the following two cases: when $\hat{\beta}_2$ and $\hat{\beta}_3$ have the same sign, prediction III is supported if $\hat{\beta}_3 \neq 0$; and when $\hat{\beta}_2$ and $\hat{\beta}_3$ have different signs, prediction III is supported if $|\hat{\beta}_3| - 2^*|\hat{\beta}_2| > 0$. "NA" under any of these columns means the respective case does not apply. Values in bold indicate support for predictions. Significant difference from zero is indicated by superscripts, and critical level of significance indicated as $** = 0.01$, $* = 0.05$, and $\cdot = 0.1$. Acronyms defined as follows: T = turnover rate, S = stems, SC = species composition, FC = functional composition, LAT = latitude, $BRAY$ = Bray-Curtis index, RAO = Rao's index, $|\Delta CWM|$ = absolute difference in community weighted mean, WD = wood density, DBH_{MAX} = maximum diameter at breast height, $SES1$ = standardized effect size from Null model 1, and $SES2$ = standardized effect size from Null model 2.

Turnover rate	Metric	Predictions			
		I	II	III	
		$\hat{\beta}_1 > 0$	$\hat{\beta}_2 + \hat{\beta}_3 < 0$	$\hat{\beta}_3 \neq 0$	$|\hat{\beta}_3| - 2^*|\hat{\beta}_2| > 0$
Stems	T_S	**0.006**[*]	0.00011	NA	−0.00069
Species composition	T_{SCBRAY}	**0.004**[·]	0.00040[**]	0.0000006	NA
Species composition	$T_{SCBRAY.SES1\_LAT}$	−1.659[*]	0.133[**]	**0.106**[·]	NA
Species composition	T_{SCRAO}[a]	**0.705**[·]	0.033	0.00331	NA
Species composition	$T_{SCRAO.SES1}$	0.228	0.047[*]	NA	0.026
Functional trait	$T_{|\Delta CWM|WD}$	0.00021	0.00001	0.000002	NA
Functional trait	$T_{|\Delta CWM|WD.SES1}$	−0.225[**]	0.016[·]	NA	0.012
Functional trait	$T_{|\Delta CWM|WD.SES2}$	−0.308	0.004	NA	−0.009
Functional trait	$T_{|\Delta CWM|DBHMAX}$[b]	0.221	−0.012	NA	0.003
Functional trait	$T_{|\Delta CWM|DBHMAX.SES1}$	0.001	−0.005	NA	0.004
Functional trait	$T_{|\Delta CWM|DBHMAX.SES2}$	0.201	−0.038	−0.031	NA
Functional trait	T_{FCRAO}[a]	**1.154**[**]	0.009	NA	−0.025
Functional trait	$T_{FCRAO.SES1}$	2.919	0.522[·]	NA	0.487
Functional trait	$T_{FCRAO.SES2}$	3.439	0.105	NA	0.078

[a] Turnover rate natural-log transformed to normalize residuals.
[b] Turnover rate square root transformed to normalize residuals.

except in a single case, for the third prediction; the unlogged forest was temporally less variable in observed turnover rates for wood density ($T_{|\Delta CWM|WD}$; See Appendix F.1 and F.2).

4. Discussion

Tropical forests store at least 40% of terrestrial carbon, process six times as much carbon as is released through fossil fuel use, and are epicenters of biodiversity (Lewis et al., 2004a). These forests are increasingly being modified by selective logging, but the extent to which this practice causes shifts in temporal dynamics of tropical forest communities remains unclear (Sist et al., 2015). Understanding the effects of selective logging on the temporal dynamics of tropical forest will help determine the extent to which tropical forests are resilient to selective logging. It will also be useful to balance the competing demands of sustainable management and conservation of tropical forests, since resilience offers insurance against loss of valued functions (Thrush et al., 2009). Succession theory offers a starting point to examine the resilience of tropical forests to selective logging. Based on this theory, we hypothesized that a tropical forest in East Africa had been undergoing recovery to pre-disturbance conditions over the 45 years after a selective logging event. We tested three predictions derived from this working hypothesis, focusing on turnover rates of three forest attributes: stems, species composition, and functional traits. Overall, we found higher turnover rates in logged than in unlogged forest for all three attributes, lending support to prediction I. However, turnover rates did not decline through time in logged forest, indicating no support for prediction II. Moreover, the unlogged forest was not less temporally variable in turnover rates than the logged forest, indicating no support for prediction III. Below we highlight some caveats before discussing the implication of these results.

4.1. Caveats

As is typical of many logging-impact studies (Lindenmayer and Laurance, 2012; Ramage et al., 2013), the logging history of vegetation study plots within Kibale is confounded with geographic space, with logged plots occupying more northerly locations than unlogged plots (Fig. 2). Previous studies on Kibale have assumed structural similarity among plots prior to logging, based on historical ground surveys that predate the logging event. These historical surveys show that the vegetation plots in this study are all located within the central block of Kibale's forests (Kingston, 1967; Bonnell et al., 2011). Nevertheless, spatial structure could create spurious relationships between forest turnover rates and selective logging, due to the effects of unmeasured space-related factors (Legendre and Fortin, 1989). The presence of spatial structure in ecological data potentially violates the assumption of independent observations, and thus may inflate degrees of freedom of classical statistical models, increasing type I error (Peres-Neto and Legendre, 2010). Here we applied a simple approach to account for this potential issue, by including the latitudinal geographic coordinates for each observation as a covariate in linear mixed effects models. This covariate was significant only for turnover rates in species composition (Appendices D and G). We emphasize that our approach to control for spatial non-independence of plots assumes a linear relationship between unmeasured spatial factors and the spatial proxy, latitude. Consequently, our approach may not account for complex non-linear spatial processes that may influence forest turnover rates independent of selective logging. This poses a potential problem for empirical tests of predictions I and III, which are based on the assumption that the logged and unlogged plot categories do not consistently differ in ways other

than in logging history. If unmeasured processes act in a non-linear, spatially structured way, then an assumption needed to test predictions I and III would be violated. However, even in that case, the test of prediction II would remain valid. The assumption in question is not required for testing prediction II because each logged plot is compared to itself in a temporal series.

There are two other potentially important limitations of this study. First, we only considered stems $\geqslant 10$ cm DBH, and therefore did not study the dynamics of small stems. Small stems are typically more numerous in most forests, and have higher turnover rates than large trees (Stephenson and van Mantgem, 2005). Also, small stem dynamics may bear the imprint of selective logging for longer than larger trees because small-sized trees are more susceptible to fine scale variations in environmental conditions and represent the regeneration potential of the forest (Decocq et al., 2014). Second, because our first census (C_1) occurred 20 years after the selective logging event, it may be argued that most successional dynamics took place before observations began. However, at C_1, plots in the logged category had lower basal area and stem density (Kingston, 1967; Chapman and Chapman, 1997, 2004) and a higher abundance of early- to mid-successional species (Bonnell et al., 2011) than those in the unlogged category, substantiating the assumption of successional differences between plot categories. These observations in our study site are consistent with the idea that successional dynamics in tropical forests may take decades (Guariguata and Ostertag, 2001; Lebrija-Trejos et al., 2010).

4.2. Prediction I: higher turnover rates in logged forest

Our results largely supported the prediction of higher turnover rates in selectively logged relative to unlogged forests for the three community attributes we studied. However, for functional traits, higher turnover rates in logged forest were apparent only when the two traits were combined into a single metric, indicating greater turnover rates in biomass for selectively logged forests. For species composition and the bivariate trait combination, this pattern of higher turnover rates in logged forest disappeared when dependencies on stem turnover were accounted for with null models (Fig. 3B–E, H and I). This lack of support for prediction I after accounting for stem turnover diverges from theoretical predictions based on the fit of organisms to their abiotic environment (Swenson et al., 2012). When observed stem and/or species turnover is accounted for, functional turnover is expected to be higher due to rapid changes in the abiotic environment following an acute disturbance and lower when the environment is relatively constant (Swenson et al., 2012). Contrary to our observations, due to more recent disturbance, higher turnover rates in logged plots should have persisted after accounting for observed stem and species turnover. Nevertheless, our results indicate that the effect of selective logging on turnover rates is largely driven by stem recruitment and mortality, consistent with the idea that succession is essentially a demographic process (Horn, 1974). Successional change following disturbance is considered the aggregated outcome of differential demographic responses of constituent species that results from interspecific variation in life history traits (van Breugel et al., 2006; Walker and del Moral, 2008). Finegan, (1996) described successional change as emerging from individualistic temporal patterns of growth and mortality that result in different species populations approaching maturity and decline at different points in succession. In the context of abandoned cornfields, van Breugel et al. (2006) demonstrate the demographic basis of succession for tropical rainforest sites in Mexico, based on higher rates of recruitment and mortality during the early stages of succession. Correspondingly, our results suggest that higher turnover rates in species composition and functional traits in
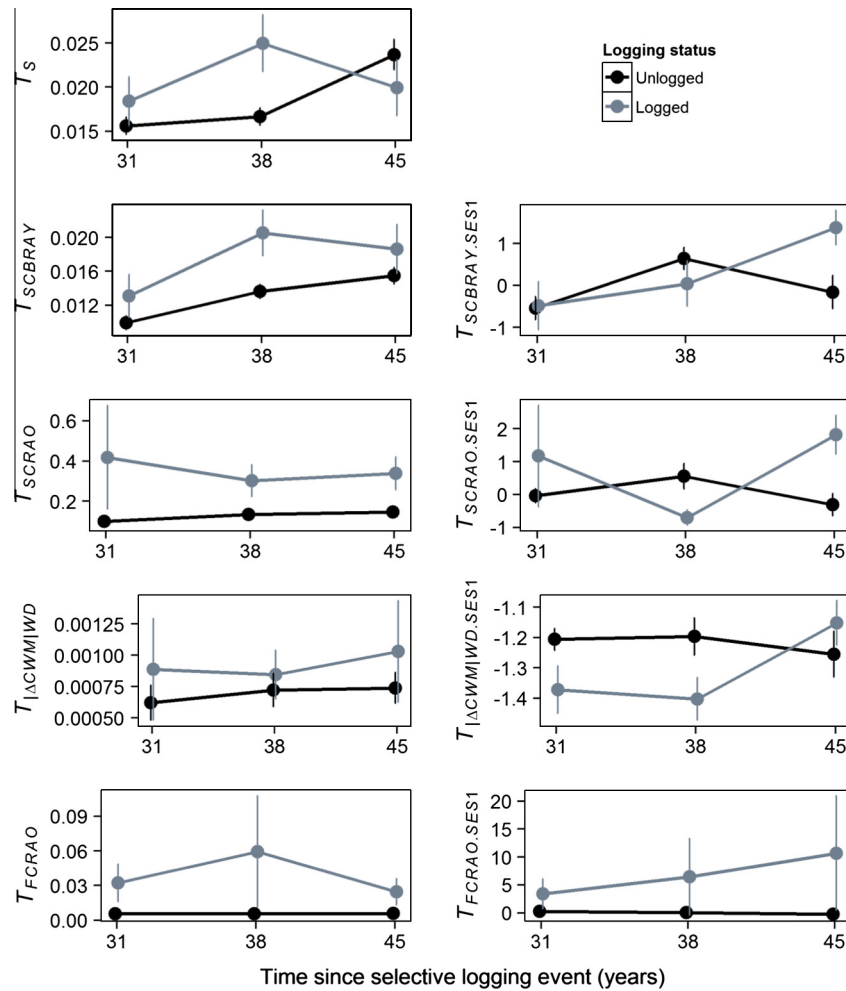
Fig. 3. Turnover rates in logged and unlogged plots at three time points since the logging event; (A) Turnover rates in stem number (T_S). (B) Turnover rates in species composition estimated with Bray–Curtis index (T_{SCBRAY}). (C) Standardized effect size (SES) for turnover rates in species composition estimated with Bray–Curtis index from null model 1 ($T_{SCBRAY.SES1}$). (D) Turnover rates in species composition estimated with Rao's index (T_{SCRAO}). (E) SES for turnover rates in species composition estimated with Rao's index from null model 1 ($T_{SCRAO.SES1}$). (F) Turnover rates in wood density ($T_{|\Delta CWM|WD}$). (G) SES for turnover rates in WD from null model 1 ($T_{|\Delta CWM|WD.SES1}$). (H) Turnover rates in the bivariate trait combination of two traits (T_{FCRAO}), WD and DBH$_{MAX}$. (I) SES for turnover rates in T_{FCRAO} from null model 1 ($T_{FCRAO.SES1}$). First census interval was from 1989 to 1999, the next census interval was from 1999 to 2006, and the last census interval was from 2006 to 2013, representing 31, 38 and 45 years since the selective logging event, respectively.

logged plots were largely driven by higher rates of stem recruitment and mortality compared to unlogged plots.

4.3. Prediction II: declining turnover rates in logged forest

Our results did not support the prediction that turnover rates decline temporally in selectively logged forests. According to this prediction, a negative slope should characterize the relationship between time since the selective logging event and turnover rates (Fig. 1), because the logged forest would be recovering from disturbance and increasing in stability as succession ensues (Horn, 1974). The absence of a decline in turnover rates through time for all three community attributes in Kibale's logged forests suggests that successional models that assume recovery to pre-disturbance structure and composition do not accurately describe the effects of selective logging on tropical forest dynamics at our site.

In contrast to prediction II, stem and functional trait turnover rates were largely constant or increased only marginally, while species composition turnover rates increased through time (Table 1, Fig. 3). The increasing temporal turnover rates in species composition were not a simple consequence of stochastic

processes of recruitment and mortality, because this increasing trend persisted after the effect of stem turnover was accounted for with null models (Table 1; Fig. 3C and E). Thus, opposite to prediction II, logged forest seemed to be increasingly unstable in terms of species composition, despite no temporal changes in turnover rates in stems and functional traits. The absence of parallel trends in turnover rates of species composition and functional traits may be explained by functional redundancy (Fukami et al., 2005; Shipley, 2010), which would imply that species' that replaced each other over the census intervals in logged plots were functionally similar. The tree species pool of Kibale is characterized by a high frequency of species with intermediate wood density values (0.5–0.75 g/cm^3), meaning there is a poor representation of species with very low wood density (<0.2 g/cm^3) that might often be colonizing pioneers and of species with very high wood density (>0.8 g/cm^3) (Chapman et al., 1999; Osazuwa-Peters et al., 2015). The high incidence of intermediate wood density species suggests that temporal change in species abundances in logged plots is not necessarily paralleled by change in functional strategies of species, resulting in relatively constant temporal turnover rates in functional traits. This scenario is illustrated in Fig. 4, which shows the relatively static distribution of wood density for all stems in
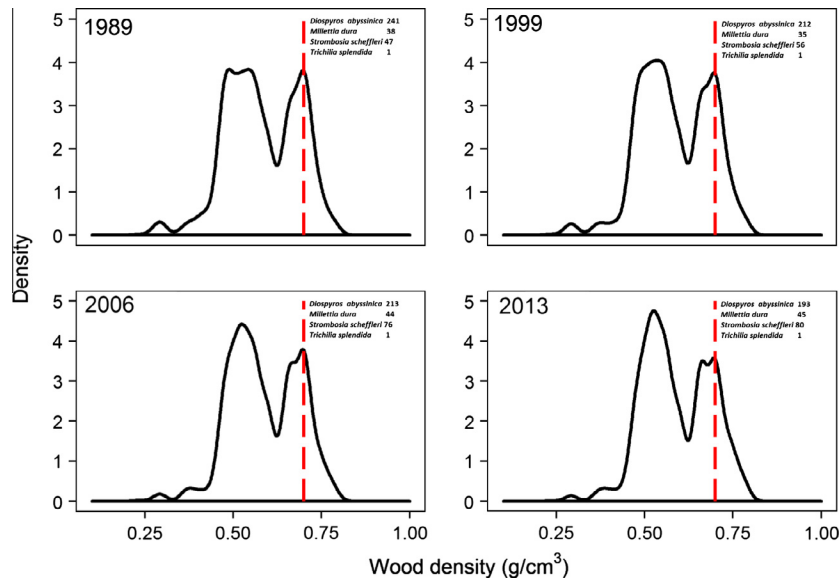
Fig. 4. Kernel density estimation showing the distribution of wood density values in Kibale at each census (1989, 1999, 2006 and 2013), where each individual in all 26 vegetation plots was assigned mean wood density values of their species. Wood density distribution remains similar across four censuses despite change in the abundance of species. As an example, notice temporal change in the abundances of the four species (top right corner of graph) with 0.7 g/cm^3 wood density (broken red line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the 26 vegetation plots, despite change in species abundances, as highlighted for four species with wood density of 0.7 g/cm^3.

4.4. Prediction III: temporally less variable turnover rates in unlogged forest

Perhaps the most surprising of our results, was the limited support for the prediction that turnover rates in unlogged forest were temporally less variable than in logged forests. The unlogged forest was expected to be temporally less variable for all three community attributes because it is considered an old-growth forest, relatively free from human disturbance in the recent past and thought to be characterized by late-successional forest dynamics (Chapman et al., 2010). Consequently, temporal patterns of turnover rates in unlogged forest would represent background or reference levels, and succession theory predicts they should be less variable than turnover rates in selectively logged forest. Only for null-model based turnover rates in species composition were the unlogged forest plots less temporally variable, providing evidence that successional changes in the taxonomic composition of selectively logged forest were in excess of background turnover rates expected from demographic processes. Temporal changes in Kibale's unlogged forest may well be part of long-term successional dynamics related to large-scale disturbance in the distant past (Chapman et al., 2010). But even if that were the case, it would seem surprising that recently (i.e., 45 years ago) logged forest was not more overtly variable than unlogged forest. An alternative explanation is that there are multiple forest-wide perturbations simultaneously operating on the vegetation in Kibale independent of the selective logging event 45 years ago. Three main sources of forest-wide disturbance in Kibale have been reported including changing rainfall patterns (Hartter et al., 2012), concentrated elephant abundance and activities (Omeja et al., 2014), and intense competition from non-tree vegetation (Duclos et al., 2013). Synergistic interactions among multiple perturbations are thought to result in long-term changes in fundamental aspects of the structure and function of biological communities (Paine et al., 1998). Such long-term changes are suggested by global trends in turnover of species composition for a wide range of taxa and biomes during the last 40 years (Dornelas et al., 2014).

5. Conclusion

Much of the focus on the effects of selective logging on tropical forests has been on the state of tropical forests at a single point in time and, to a lesser extent, on the temporal dynamics of stems or species composition. Here, we simultaneously investigated the effect of selective logging on tropical forest dynamics in stems, species and functional trait composition, while accounting for interdependencies among these three kinds of community dynamics using null models. The main take home message from our study is that classical successional models that assume recovery to pre-disturbance conditions seem inadequate for predicting the effects of selective logging on the dynamics of the tropical forest in Kibale. We found no empirical support for decline in turnover rates through time following selective logging. Stem and functional turnover rates in logged forest plots did not show significant temporal trends, in contrast to turnover rates in species composition that increased linearly with time since logging. Lastly, many of the temporal turnover rate patterns were driven primarily by stem turnover rate, with the exception of temporal increases in species composition turnover rates, which remained after accounting for the effect of stem turnover.

Future work may be aimed at determining the generality or uniqueness of our results from Kibale, based on similar studies in tropical forests elsewhere, avoiding when possible confounding spatial location and logging history. Succession is thought to be driven by short-term local drivers (e.g. plant life cycles, nutrient fluxes, and herbivory), but constrained by long-term regional processes such as species pool dynamics (Walker and Wardle, 2014). Consequently, results in this study may be shaped by Kibale's specific ecology and constrained by the history of African tropical forests including a relatively small regional species pool and historically few and small disturbances as compared to other tropical regions (Richards, 1996; Chapman et al., 1999).

Nevertheless, our results lead to the conclusion that tropical forests are not as resilient to selective logging effects as widely thought (Putz et al., 2012; Edwards and Laurance, 2013). Selective logging resulted in persistently higher turnover rates in Kibale's forest, which may compromise its carbon storage capacity. Selective logging effects may also interact with effects from other

global change trends, particularly climate change. The synergistic effects of multiple perturbations could potentially cause major long-term shifts in the dynamics of tropical forests. Ultimately, the view that selective logging is a benign approach to the management of tropical forests should be reconsidered in the light of the studies on the effects of this practice on long-term forest dynamics.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.08.002.

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