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How persistent are the impacts of logging roads on Central African forest vegetation?

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Summary

1. Logging roads can trigger tropical forest degradation by reducing the integrity of the ecosystem and providing access for encroachment. Therefore, road management is crucial in reconciling selective logging and biodiversity conservation. Most logging roads are abandoned after timber harvesting; however, little is known about their long-term impacts on forest vegetation and accessibility, especially in Central Africa.

2. In 11 logging concessions in the Congo Basin, we field-sampled a chronosequence of roads that, judging from satellite images, had been abandoned between 1985 and 2015. We assessed recovery of timber resources, tree diversity and above-ground biomass in three zones: the road track, the road edge (where forest had been cleared during road construction) and the adjacent logged forest.

3. The density of commercial timber species <15 cm d.b.h. was almost three times higher in the road track (321 individuals ha^{-1}) and edge (267) than in the logged adjacent forest (97). Over time, tree species diversity converged to a comparable level between roads and adjacent forests, along with an increase in canopy closure.

4. The average width of forest clearing for road construction was 20 m, covering a total 0·76% of the forest area inside concessions. After 15 years following abandonment, road tracks had recovered 24 Mg ha^{-1} of above-ground woody biomass, which was 6% of that in the adjacent forest, while road edges had accumulated 167 Mg ha^{-1} (42%). Ten years after abandonment, roads were no longer penetrable by poachers on motorcycles. An exotic herb species was fully replaced by dominant Marantaceae that have even higher abundance in the adjacent forest.

5. *Synthesis and applications*. Our evidence of vegetation recovery suggests that logging roads are mostly transient elements in the forest landscapes. However, given the slow recovery of biomass on abandoned road tracks, we advocate both reducing the width of forest clearing for road construction and reopening old logging roads for future harvests, rather than building new roads in intact forests. Road edges seem suitable for post-logging silviculture which needs to be assisted by removing dominant herbs during the early years after abandonment while the road track is still accessible.

Key-words: biomass, Congo Basin, invasive herbs, rain forest resilience, regeneration, road ecology, selective logging, soil compaction, sustainable forest management, tree diversity

Introduction

Large parts of the world's humid tropical forests are selectively logged (Asner *et al.* 2009), and there is an urgent need to reconcile this method of exploitation with biodiversity conservation (Edwards *et al.* 2014). A key element in reducing selective logging impacts is management of the extensive road networks built into the forest (Mason & Putz 2001). Road construction requires full clearance of narrow linear sections of the forest area, with far-reaching consequences for the forest ecosystem

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*Correspondence author. E-mail: fritz.kln@gmail.com through fragmentation, desiccation and spread of invasive species (Laurance, Goosem & Laurance 2009). Despite bringing potential benefits to local people, frontier roads in remote forests are therefore mostly considered to threaten biodiversity conservation especially due to their widespread use by bushmeat hunters (Wilkie *et al.* 2000; Laurance 2001).

On a global-scale road map, major parts of Central Africa have been classified as a priority road-free area due to their species richness and high carbon stocks (Laurance *et al.* 2014). However, logging road networks in the Congo Basin have been expanded greatly over the last 20 years (Laporte *et al.* 2007) to gain access for selective logging of a few, high-value timber species, notably sapelli *Entandrophragma cylindricum* (Sprague) (Karsenty & Gourlet-Fleury 2006). Up to 53% of the biomass of this valuable species has been harvested in one concession (Gideon Neba *et al.* 2014), likely depleting the available timber stock (Hall *et al.* 2003). Forest clearing for road building in selective logging operations also causes carbon emissions (Putz *et al.* 2012), but the magnitude of this contribution and the extent to which the carbon is recaptured during subsequent vegetation recovery remain unclear.

Not all timber extraction roads have the same impact. Secondary logging roads, only used to transport logs from where they were cut to a main road, are usually abandoned immediately afterwards (Malcolm & Ray 2000). On Landsat images, they are detectable with bare soil for an average of 4 years and covered with vegetation for 20 years before they are no longer distinguishable from surrounding forest (Kleinschroth *et al.* 2015). Only 12% of roads in forest concessions observed over the last 15 years have been permanently open (Kleinschroth, Healey & Gourlet-Fleury 2016). Abandoned logging roads have been characterized as long-lasting, relatively floristically uniform and structurally altered long corridors that may have particular ecological functions in selectively logged forests (Guariguata & Dupuy 1997). Especially in areas where high volumes of timber are harvested, such as the dipterocarp forests of South-East Asia, reduced levels of regeneration have been reported on abandoned roads and skid trails due to unfavourable soil conditions such as compaction and low nutrient content (Pinard, Barker & Tay 2000; Zang & Ding 2009). In contrast, for regions with low-intensity logging regimes in South America, logging roads and strip clearcuts have been associated with enhanced levels of regeneration of light-demanding timber species (Hartshorn 1989; Fredericksen & Mostacedo 2000; Nabe-Nielsen *et al.* 2007). Few comparable studies exist for Central Africa; however, Malcolm & Ray (2000) reported reduced sapling densities and tree species richness on and alongside abandoned logging roads compared with unlogged forests. In Central Africa, harvesting intensity is generally low (1–2 trees per ha, Karsenty & Gourlet-Fleury 2006) and roads are the most costly and destructive components of logging operations (Mason & Putz 2001); their long-term management is thus crucial for impact reduction.

The existing studies about forest regeneration on abandoned logging roads are mostly based on small sample sizes with limited spatial and temporal coverage. In contrast, we used remote sensing information (Kleinschroth *et al.* 2015) to identify roads abandoned over a continuous chronosequence of dates between 1 and 30 years ago, spanning a large area (25 000 km^2) and different geological substrates. This study investigates the trajectory of vegetation succession and environmental conditions after logging road abandonment to find out how long-lasting are the threats of roads to forest ecosystems due to low recovery rates after logging disturbance and resulting persistence in fragmentation. We assessed recovery in terms of regeneration of commercial timber species, tree species diversity and aboveground woody biomass (AGB) and linked this with soil condition, herb cover and reduced accessibility to poachers. From this evidence, we suggest how the resilience of forest landscapes can be incorporated into better road management strategies to enable more sustainable forest exploitation and effective restoration.

Materials and methods

STUDY AREA

The catchment of the Sangha River, a major tributary of the Congo, has been subject to widespread logging activity. In order to cover a broad range of its forests, we selected 11 logging concessions, owned by four different companies (Alpi, OLAM, Rougier, Decolveneaere), in the Eastern province of Cameroon (centred at 3°43′26″N 14°36′58″E) and the Sangha and Likouala provinces of Republic of Congo (centred at 1°51′18″N 16°25′01″ E). The total area of all 11 studied concessions is 25 049 km^2 located within a total forest area of ca. 100 000 km^2 (Fig. 1). The area's logging history is long with some concessions dating back to the 1960s, while in others logging started only after 2000 (Laporte *et al.* 2007). The forest is mostly semi-deciduous and altitude range is 350–650 m. All 11 concessions are certified by Origine et Légalité des Bois, and four of them are certified by the Forest Stewardship Council. All are operating according to a forest management plan that includes the assignment of annual felling areas (*assiettes annuelles de coupe*, AAC).

STUDY DESIGN

Using a time series of LANDSAT images, we identified a chronosequence of roads abandoned between 1985 and 2015 (Fig. 1). As all the roads are in dedicated logging concessions, we assumed that they had been built for logging purposes. We defined road abandonment as a state shift from being actively used by cars and trucks to being in the process of revegetation. The years of road use were indicated by the presence of bare soil. Given the differences in spectral properties between bare soil and recovering vegetation the first year when a road was abandoned could be determined based on the difference between the red and near-infrared channels on the LANDSAT images (Kleinschroth *et al.* 2015). For the time before 1997, images were not available at regular intervals and some roads could only be detected after they had already been abandoned. In these cases, we assumed

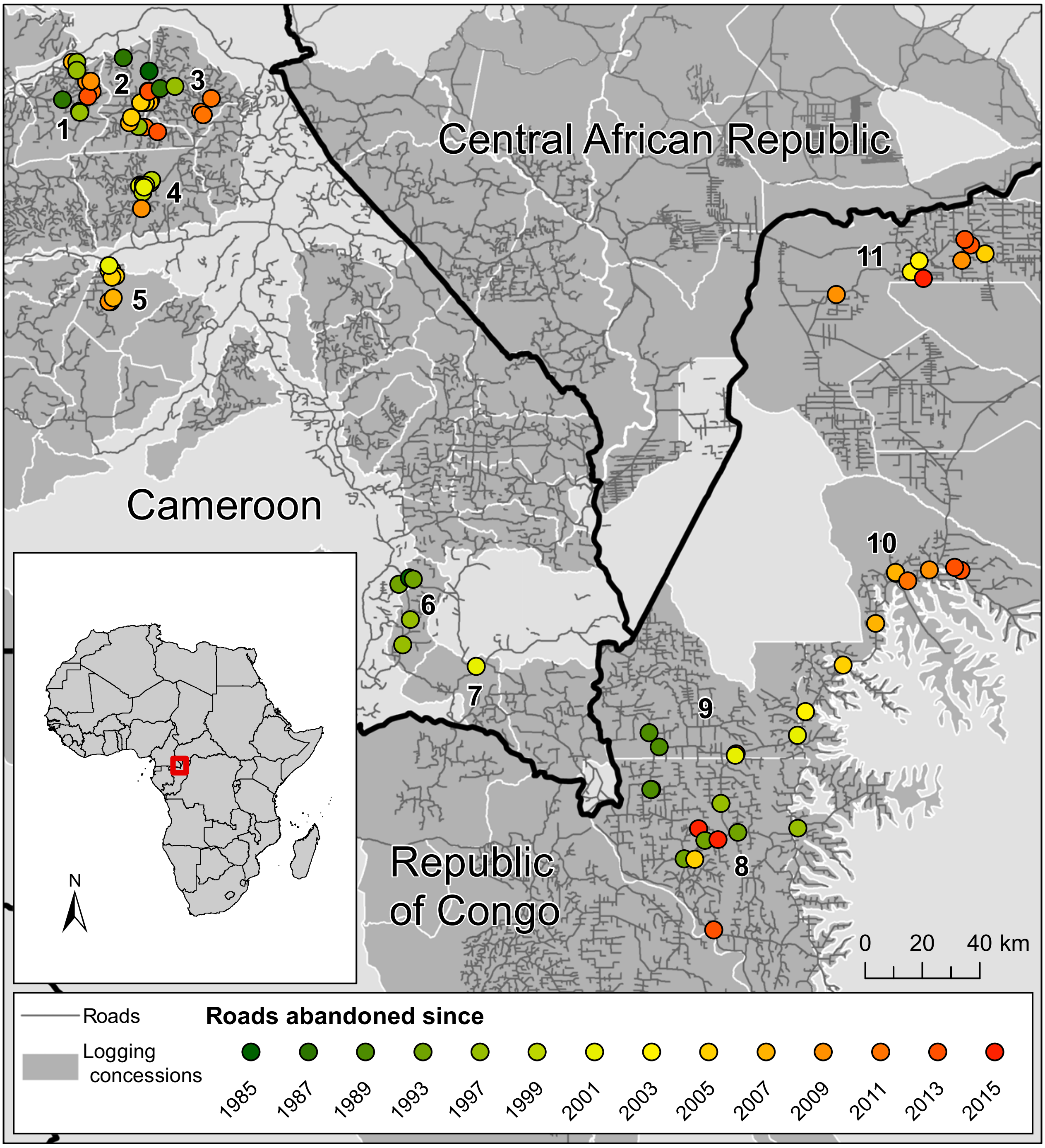

Fig. 1. Map of the 86 roads sampled in the study. Colour gradient from green to red depending on time of abandonment based on interpretation of Landsat images. White lines indicate concession boundaries; sampled concessions are consecutively numbered.

that road activity had ceased in the preceding year. The study area is covered by four LANDSAT scenes (P183, RR57-58, P182, RR58-59). We used the whole range of images available on http://glovis.usgs.gov, covering images of LANDSAT 5, 7 and 8 (all 30-m pixel size). Due to differences in image availability and quality, more than 130 images were grouped and processed together in the following intervals: before 1986, 1986–1987, 1988–1989, 1990–1993, 1994–1997, 1998–1999, 2000–2001, 2002–2003, 2004–2005, 2006–2007, 2008–2009, 2010–2011, 2012–2013, 2014–2015. We corrected the final road map with the World Resources Institute forest atlases of Cameroon and Congo that include the AAC felling areas for each year (http://www.wri.org/our-work/project/congo-basin-forest-atlases). The accuracy of the road map was continuously tested while travelling over ~2000 km of roads in the study area, using a mobile GIS, comparing the interpretation of recent images with the situation on the ground.

PLOT DESIGN

On each of a randomized sample of 86 roads, within strata based on year of road abandonment, we laid out two 50-m gradient-

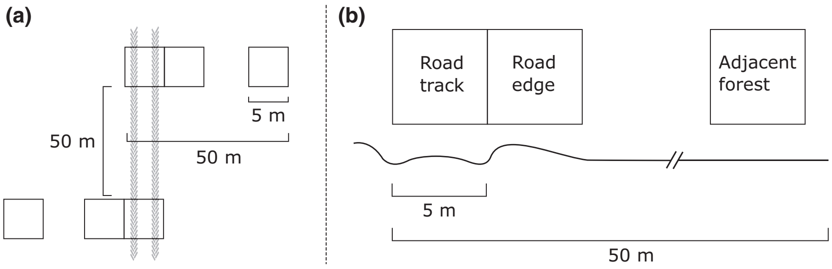

Fig. 2. Plot design with the location of subplots (a) in plan-view on and alongside the abandoned road and (b) as a cross-section from the road track into the adjacent forest showing the profile of the soil surface.

directed transects (gradsects, Gillison & Brewer 1985), separated by 50 m and each perpendicular to the opposite side of the abandoned road (Fig. 2a). This form of sampling across a steep environmental gradient has been shown to be accurate and more effective than fully random designs and to be useful in regression-type analyses in tropical forests (Parker *et al.* 2011). We adapted the transect design so that each contained three subplots of 5 × 5 m placed systematically in three parallel zones on a gradient of road-related disturbance (Fig. 2b). The road track was characterized by the removal of top soil and sometimes the application of a surface cover of laterite to facilitate traffic (Sessions 2007). It was demarcated by accumulated soil embankments on both sides (Guariguata & Dupuy 1997). In 16% of the plots, the road track was <5 m wide and so included up to 1 m of the opposite edge. The road edge is the area on both sides of the track that had been cleared of all vegetation to allow the sun to dry the road surface (Sessions 2007). It was characterized by accumulated soil from road building. The adjacent forest was more-or-less old growth but showed occasional signs of selective logging. Slash from vegetation cleared during road construction was found to be removed to the adjacent forest, but no systematic piling of slash was apparent. The road track and edge zones were directly adjacent to each other, with the former roadside ditch marking the border. The forest subplot was placed selectively beyond the edge zone at the first position along the transect with no more visible influence from the former road. This was on average 41·7 m away from the road track. The design was fully balanced among the three zones with two triplets of plots per sample site (Fig. 2 a). The small size of the subplots is adapted to inventorying the early succession stages on the narrow road track and edge and is less suitable for the characterization of mature forest. The third subplot therefore serves more as a coarse reference. A detailed description of the data collection and all variables recorded is provided in Appendix S1 (Supporting information).

STATISTICAL MODELLING

We applied data exploration following the protocol of Zuur, Ieno & Elphick (2010), using Cleveland dotplots to inspect the variables for outliers and pairwise scatterplots to assess collinearity. We strictly avoided collinearity among the covariates. This approach led us to use a fixed set of variables comprising time after abandonment, clearing width, road habitat zone and geological substrate for all models. To avoid heteroscedasticity, we applied log transformation, combined with adding a constant of 0·01 to all basal area and AGB variables. Due to a high number of plots without observations of commercial species, we fitted two different models to explain the regeneration of commercial trees: (a) frequency of presence/absence and (b) basal area of only those commercial species ≥1 and <15 cm d.b.h. that were present. Each subplot was treated as a replicate. To avoid pseudo-replication, sites located inside the same felling area (AAC) were assumed to be non-independent. To take account of this nested design, we included AACs as random factors in a mixed-effects regression model. The 86 roads sampled were distributed over 63 AACs. We used generalized linear-mixed models (GLMM) for the presence/absence of commercial species with Bernoulli distribution and linear-mixed models (LMM) for the normally distributed variables, Shannon diversity index, log-transformed basal area and AGB. There is ongoing debate about the use of *P*-values in such models (Pinheiro & Bates 2000); therefore, we applied a bootstrapping procedure with 100 replications to construct confidence intervals. Only if 0 did not fall within the 95% confidence interval was the variable assumed to be significant (Fig. 3, Table S1). An increase of the bootstrap replications up to 1000 did not produce any difference in the results. We calculated floristic dissimilarity between groups of plots using the incidence-based Jaccard and abundance-based Morisita–Horn indices (Magurran 2004). The Jaccard index was visualized using Kruskal's non-metric multidimensional scaling (NMDS). To compare the presence of paths with age of road, we used nonparametric Kruskal–Wallis tests with Mann–Whitney *U*-test statistics (Wilcoxon rank-sum test) as *post-hoc* tests. All analyses were carried out in R (R Core Team 2014), using the packages 'vegan', 'lme4', 'boot' and 'ggplot2'.

Results

REGENERATION OF COMMERCIAL SPECIES

Of the total number of 173 recorded tree genera, we identified 26 species (among 35 potential ones) that have commercial timber value (Appendix S1). Their combined density was 321 individuals <15 cm d.b.h. ha^{-1} in the road track and 267 in the edge zone, compared with 97 trees <15 cm d.b.h. ha^{-1} in the adjacent forest. There were five individuals ≥15 cm d.b.h. ha^{-1} in the road track, 24 in the edge and 63 in the forest (Table S2). The frequency of commercial species individuals <15 cm d.b.h. was higher in the road track (45·3% of plots, $P < 0{\cdot}001$) and in the edge (37·7%, $P < 0{\cdot}001$) than in the adjacent forest (19·3%, Figs 3 and 4). The presence-only model for the log-transformed basal area of commercial species individuals <15 cm d.b.h. showed no difference between the road habitat zones but a significant positive trend with time after abandonment ($P = 0{\cdot}001$, Fig. S1). Road edges abandoned >15 years ago had the highest basal area of timber species recruits (Mean ± CI: 0·74 ± 0·55 m^2 ha^{-1}) followed by the road track (0·54 ± 0·31), both higher

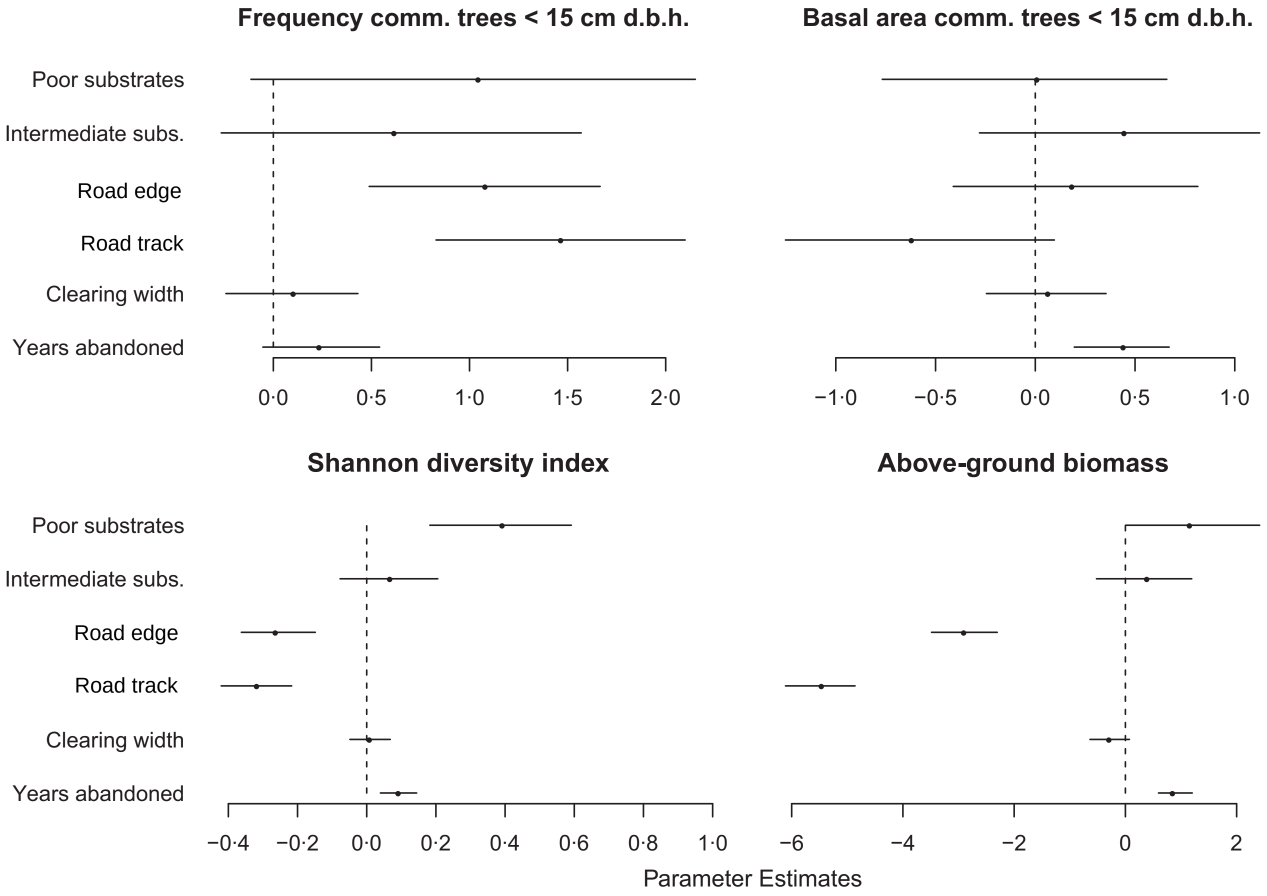

Fig. 3. Effects of substrate (poor, intermediate), habitat zone (road track, edge), clearing width and time (years after abandonment) on frequency and basal area of individuals <15 cm d.b.h. of commercial tree species, Shannon diversity index and above-ground biomass. Effect sizes are results from linear-mixed models (for frequency: generalized linear-mixed model) with AAC as a random effect, and are presented with 95% CIs; those that do not overlap the dashed vertical line are statistically different from zero. Negative values indicate negative correlations, positive vice-versa.

than in the adjacent forest (0·16 ± 0·14) due to a decreasing trend over time (Fig. 4).

TREE DIVERSITY

The Shannon diversity index of tree genera for individuals ≥1 cm d.b.h. was significantly lower in road track and edge zones (both $P < 0{\cdot}001$) than in adjacent forest. However, diversity increased significantly over time ($P = 0{\cdot}001$), with the greatest increase taking place in the road track (from 0·25 ± 0·12 on roads <8 years old to 1·1 ± 0·17 in roads >15 years old), while it did not change in the adjacent forest (from 1·24 ± 0·14 to 1·15 ± 0·17, Fig. 4). Poor substrates had a higher Shannon diversity index than rich ones ($P < 0{\cdot}001$, Fig. S2). Floristic dissimilarity based on the Jaccard index and visualized through NMDS was pronounced between the three zones for roads abandoned <8 years ago. With age since road abandonment, species composition in adjacent forest stayed very similar, while that in road track and edge zones remained distinct from the forest only on the first axis but underwent a clear development towards the forest on the second axis (Fig. S3, Table S4). Basal area in all zones was mostly composed of pioneer tree species such as *Musanga cecropioides* (R. Br.) that thrived particularly in road edges (Fig. 4). Fifteen years after road abandonment, pioneer species accounted for 70% of the basal area in road tracks and 56% in edges. Only in the adjacent forest was the dominance of pioneer species reduced to 32%, replaced by non-pioneer light demanders with shade bearers remaining at a similar level (Fig. 5). Due to the small plot size, species accumulation curves did not reach their saturation limit throughout all groups of samples (Fig. S4).

BIOMASS

Above-ground biomass was significantly lower in road track and edge zones (both $P < 0{\cdot}001$) than in the adjacent forest, but the log-transformed AGB increased significantly with time after road abandonment ($P < 0{\cdot}001$, Fig. S5). For the road track, this meant an increase from 1·3 ± 1·3 Mg ha^{-1} on roads abandoned <8 years ago to 24·0 ± 19·35 Mg ha^{-1} on those >15 years and for the road edge an increase from 78·3 ± 73·38 to 166·67 ± 166·67 Mg ha^{-1} (Fig. 4). Of the total studied concession area, 190 km^2 (0·76% of the forest cover) was

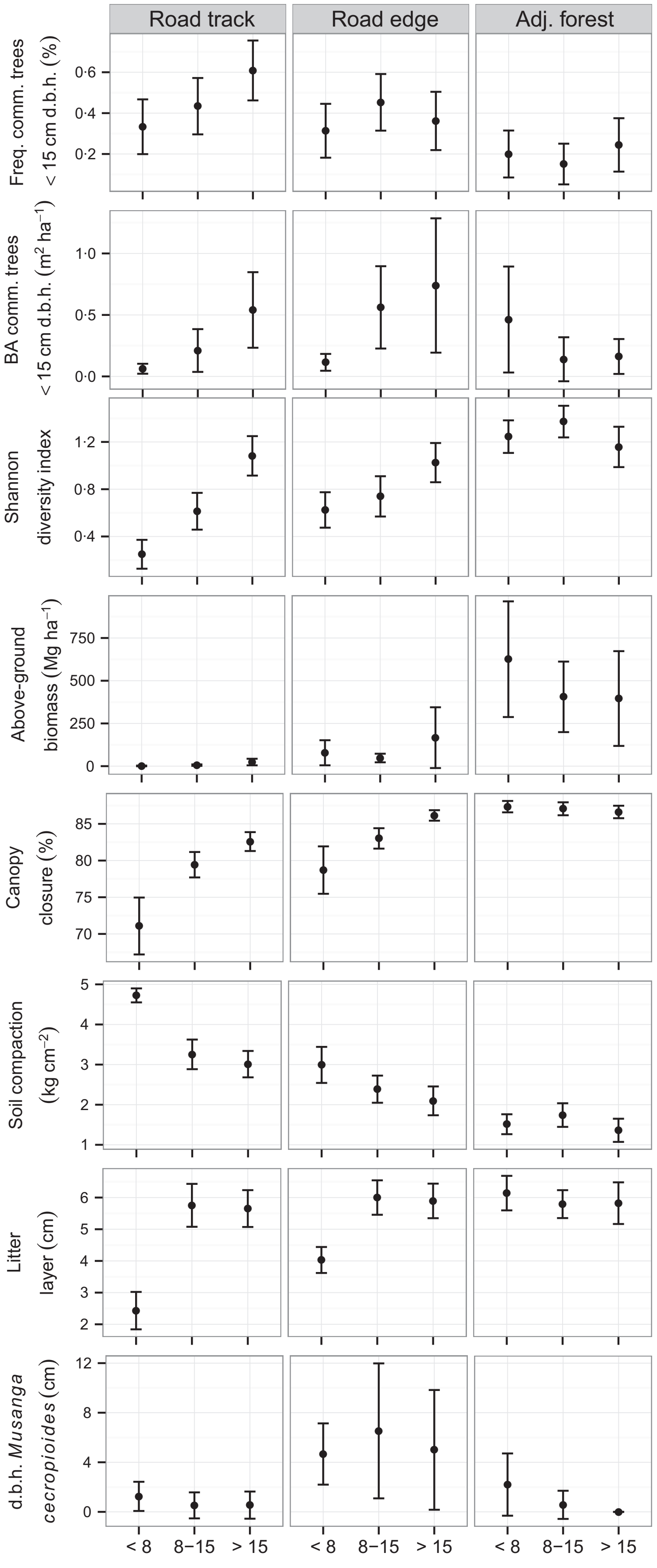

Fig. 4. Mean values and 95% confidence intervals for eight variables (horizontal) across plots in three habitat zones (vertical) and three road age categories (inside each box). Freq., frequency of presence/absence; BA, basal area of commercial species that were present; d.b.h., diameter at breast height. The sample size for each point lies between 44 and 53.

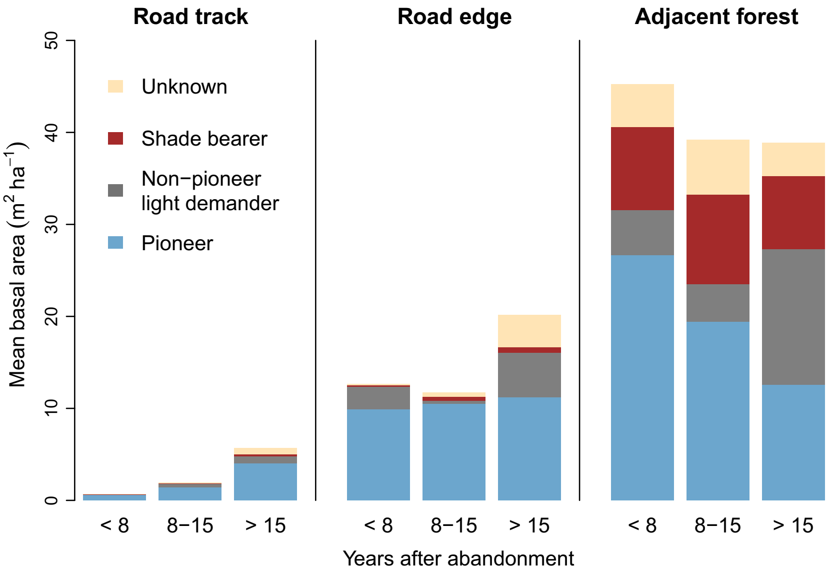

Fig. 5. Mean plot values of basal area of tree species regeneration guilds over age since road abandonment, in each of the three habitat zones. The unknown group consists of trees that could not be identified or those of genera that could not be assigned to a guild based on available literature and expert knowledge.

cleared for road construction during 1985–2015 (Table S3). This amounts to ca. 7 500 965 Mg AGB lost through road construction, or 790 Mg km^{-1}. The amount of biomass recovered through forest regrowth on road tracks older than 15 years amounts to 138 323 Mg, which is 6% of the initial amount cleared, while road edges regained 2 174 856 Mg (42%).

CANOPY CLOSURE AND SOIL CONDITIONS

All of the environmental variables (canopy closure, soil compaction and thickness of the litter layer) were strongly correlated with the gradient between the three zones from road track to adjacent forest and with road age (Fig. 4). Canopy closure was lower in road track and edge (both $P < 0{\cdot}001$) than the adjacent forest, but it increased significantly with road age ($P < 0{\cdot}001$) such that it was very similar at ca. 80–90% in all three zones after 30 years (Fig. S5). Canopy closure was negatively correlated with clearing width ($P = 0{\cdot}006$). The litter layer showed similar patterns with lower values in the road track ($P < 0{\cdot}001$) and edge ($P = 0{\cdot}005$) than the forest, differences that are eliminated by 30 years due to the significant increase over time ($P < 0{\cdot}001$). Soil compaction was higher in the road track ($P < 0{\cdot}001$) and edge ($P < 0{\cdot}001$) than the forest, but these differences were reduced by the significant decrease over time ($P = 0{\cdot}001$), especially in the road track (Fig. S5). However, the value after 15 years was still more than twice as high in the road track (3·01 ± 0·33 kg cm^{-2}, Fig. 4) as in the forest (1·36 ± 0·29). Soil compaction was lower on poor (1·23 ± 0·49, $P < 0{\cdot}001$) and intermediate (2·06 ± 0·27, $P < 0{\cdot}001$) substrates than on rich ones (2·92 ± 0·16, Fig. S2, Table S1).

HERBACEOUS SPECIES

The ground cover of the herbaceous non-native species *Chromolaena odorata* ([L.] R. M. King & H. Rob.) on the road track decreased rapidly with time after road abandonment ($P = 0{\cdot}001$), from 18 ± 7·91% in the < 8-year-old roads to 1 ± 1% after 15 years (Fig. 6). On the road edge, its mean cover was 5·8 ± 4·77% immediately after road abandonment and decreased to being absent after 8 years. Clearing width had a positive effect on the cover of *C. odorata* ($P < 0{\cdot}001$). In road track and edge zones, the genus *Aframomum* (K. Schum.) was more abundant than in the adjacent forest ($P < 0{\cdot}001$), but showed no strong trend with road age. The cover of Marantaceae increased over time across the zones ($P < 0{\cdot}001$) and after 8 years since road abandonment they were always the dominant herbaceous plant group with a mean cover of 35%. Their cover was significantly lower in the road track than the adjacent forest ($P = 0{\cdot}002$). Cover of both Marantaceae and *Aframomum* spp. was significantly lower on poor (3% and 5%) than rich soils (31% and 19%, $P = 0{\cdot}004$ and $P = 0{\cdot}015$, respectively, Fig. S2, Table S1).

ACCESS FOR BUSHMEAT HUNTING

Of all the roads sampled, 56% did not show any sign of a path used by hunters, 26% were used as footpaths and 18% by motorcycles. The presence of footpaths was independent of road age, but on roads abandoned more than 10 years ago, we did not find any paths used by motorcycles because fallen trees, broken bridges and vegetation density made passage impossible. The age of roads with motorcycle paths was significantly lower than those with footpaths or no path at all (Fig. S6).

Discussion

Our results indicate that abandoned logging roads present only a transient threat to the structural integrity of forest in the northern Congo Basin due to rapid recovery in timber stocks and tree diversity. This contrasts with earlier studies in Latin America (Guariguata & Dupuy 1997;

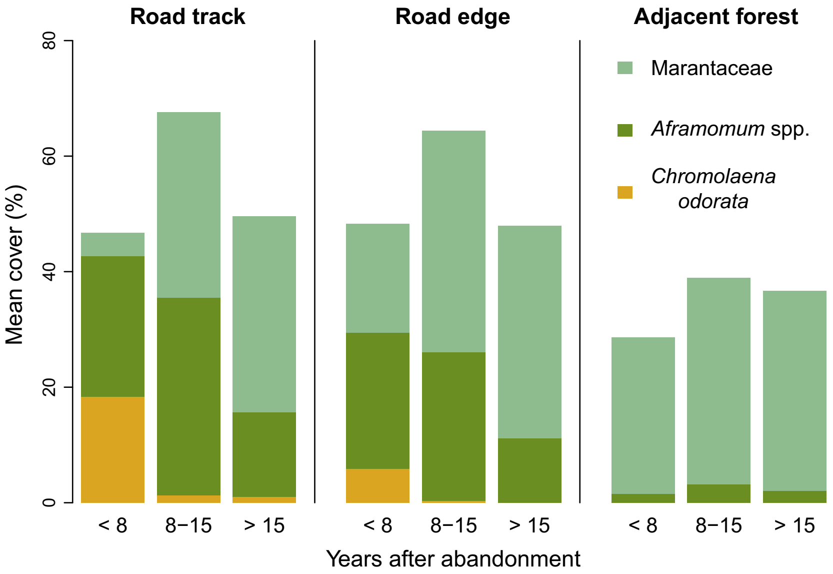

Fig. 6. Mean plot values of cover of three dominant groups of herbaceous plants over time after road abandonment, in each of the three habitat zones.

Olander, Scatena & Silver 1998), South-East Asia (Pinard, Barker & Tay 2000; Zang & Ding 2009) and Central Africa (Malcolm & Ray 2000). While 30 years of regeneration were not sufficient to accumulate the same level of biomass on roads as in adjacent logged forest, canopy closure, litter layer depth and herb cover converged notably. With the exception of the dense forests on poor sandstone substrates in the northern Republic of Congo, all forests in the study area have a relatively open canopy, with high ground cover of Marantaceae herbs. This forest structure has been attributed to disturbances 2500 years ago (Maley 2002) potentially linked to agricultural colonization (Bayon *et al.* 2012) followed by arrested succession. With these long-term degraded forests as a reference, there is a great capacity for forest recovery on abandoned logging roads through natural processes. We showed a clear convergence of forest structure with the surrounding old-growth forest, similar to the findings of Norden *et al.* (2009). Forest opening for road construction has been considered the most important driver of forest degradation resulting from selective logging, but, in contrast, our study does not characterize roads as triggers of a permanent regime shift in the sense of Folke *et al.* (2004). Therefore, the presence of a temporary logging road at one point in time cannot be equated with long-term forest degradation in general. This disturbance does not exceed the resilience capacity of the forest ecosystem.

ROADS FAVOUR RECRUITMENT OF TIMBER SPECIES AND RECOVERY OF BIODIVERSITY

The frequency of commercial timber species regeneration was higher in road track and edge zones than adjacent forest, as has been shown for logging roads in Bolivia (Fredericksen & Mostacedo 2000; Nabe-Nielsen *et al.* 2007) and strip clearcuts in Peru (Hartshorn 1989). More than 50% of the timber species found, including the most-valued *Entandrophragma cylindricum,* are classified as non-pioneer light demanders (Hawthorne 1995). Absolute numbers were very low, as only 23 individuals <15 cm d.b.h. of *E. cylindricum* were recorded across all three habitat zones and in 17 of the study sites. This regeneration was despite the absence of even a single tree ≥15 cm d.b.h. of this species in the 1·55 ha of forest sample plots across the 11 studied concessions. We attribute this regeneration to the open environment of the area cleared for roads, given that seedlings of *E. cylindricum* grow well in the light conditions of small- and intermediate-sized gaps (Hall *et al.* 2003).

Concurrent with commercial species recovery, we noted an increase in tree diversity, reaching a similar level in the road zones to the forest after 30 years. Road edges have been identified as particularly suitable for tree recruitment both in Central America (Guariguata & Dupuy 1997) and Central Africa (Doucet 2004) due to the most valuable commercial species in both regions tending to be strongly light-demanding and this habitat offering both high light levels and an accumulation of topsoil from road construction. We found similar levels of commercial tree species regeneration in road track and edge zones, along with a reduction in soil compaction with age since road abandonment. The growth of diverse light-demanding tree species in the open road zones can be attributed to the combined effects of soil recovery, light availability and reduced herb competition (Marantaceae herbs had a lower mean cover on the road track than in the adjacent forest). On both the road track and edge, tree communities underwent a large turnover of notably distinct assemblies of genera with age since abandonment. Pioneer tree species remained dominant in basal area throughout the 30 years, but in the adjacent logged forest, we found a reduction in their basal area followed by an increase in that of non-pioneer light-demanding species, which corresponds with the expected trend of forest recovery from disturbance (Finegan 1984). At the same time, both Shannon diversity and floristic dissimilarity in the forest remained at the same level over age since logging. These results indicate that recovery of the tree community on abandoned roads follows a faster trajectory than the adjacent logged forest.

PRONOUNCED DIFFERENCES IN BIOMASS RECOVERY

The total amount of forest clearance for road construction over 30 years in the 25 000 km^2 area of the 11 studied forest concessions resulted in approximately $13{\cdot}8 \times 10^6$ Mg CO_2 being emitted to the atmosphere (assuming 50% carbon content of woody biomass). This is equivalent to the emissions of 55 000 UK citizens over the same time period (based on 250 Mg per person over 30 years, http://data.worldbank.org). Approximately 30% of this emitted CO_2 has been recaptured through regeneration on these roads during the 30 years. However, we found strong contrasts in recovery of above-ground woody biomass between the habitat zones. Despite its increase over time, biomass on the road tracks had only recovered to 6% of the average forest level between 15 and 30 years after road abandonment. Assuming linear recovery on road tracks, it would take at least 300 years until biomass stocks reach the level of adjacent forest. This estimation is at a comparable level to the results from a study in Puerto Rico (Olander, Scatena & Silver 1998) but is an even slower rate of recovery than that found for basal area on old skid trails and gaps after logging in Ghana by Hawthorne *et al.* (2012). In contrast, on road edges, with less compacted topsoil, tree basal area and canopy closure recovered much faster. Here, the accumulation of biomass during the first 30 years was dominated by fast-growing pioneer species such as *Musanga cecropioides*. Projection of future development of biomass needs to consider the short life span of pioneer species and their replacement by more shade-tolerant denser wooded species (Finegan 1984), even though this had not yet occurred up to the 30 years since abandonment of the oldest road in our study.

CANOPY CLOSURE AND HERB COVER CONVERGE BETWEEN ROADS AND ADJACENT FORESTS

We showed that <1% of the forest area had its canopy cover cleared for the construction of logging roads. However, we consider the average clearing width of 20 m (range 8·5–40·5) for road constructions excessive, as evidence from Brazil shows that logging roads can be operated at average clearings that are half as wide (Feldpausch *et al.* 2005). Nonetheless, even with a 20 m width the opening is only short term, with canopy closure recovering to 83% (very close to the value in the adjacent forest) ca. 25 years after road abandonment. The extent to which roads present an obstacle for the movement of mammals (Blake *et al.* 2008) is likely to reduce over this same time-scale. Recovery of canopy cover was slowest on roads with the greatest initial width of clearance for road construction, which may be linked to the rapid establishment and persistence of a high level of cover of competitive herbaceous species restricting subsequent rates of tree establishment, especially of light-demanding species. Honu & Dang (2002) suspected that the non-native *Chromolaena odorata* impedes regeneration of valuable timber species, but our results showed that on abandoned logging roads *C. odorata* remained abundant for <8 years, after which it declined to a very low level due to the shading of canopy closure and regrowing woody plants (Witkowski & Wilson 2001). However, not all robust herbaceous species declined over the same time-scale. Instead, there was a marked turnover, with *Aframomum* species increasing in abundance after 8 years but declining after 15, whereas Marantaceae species were dominant after 15 years, reflecting their high abundance across large areas of forest landscape in the region (Brncic *et al.* 2009). The abundance of these highly competitive herbaceous species will be a major persistent factor regulating the regeneration of tree species after logging, both on roads and in the forest.

CONTRASTING SUCCESSIONAL TRAJECTORY ON POOR SANDY SOILS

We detected spatial patterns in forest structure and timber species recruitment at a large scale linked to underlying geology. The sandstone plateau in northern Republic of Congo characterized by deep resource-poor soils features a generally older, less-disturbed and slower growing forest type (Fayolle *et al.* 2012). Here, roads tended to remain detectable for longer than in more disturbed forests on rich substrates (Kleinschroth *et al.* 2015). However, over the 12 years after road abandonment studied here on these poor soils, overall tree diversity was higher than on the intermediate and resource-rich soils in other parts of the study area. The different trajectory of succession on the poor sandy soils can be associated with their lower soil compaction and especially much lower abundance of competitive dominant herbs.

HOW LONG DO LOGGING ROADS REMAIN ACCESSIBLE FOR BUSHMEAT HUNTERS?

Logging in the study region is nearly always accompanied by hunting (Poulsen, Clark & Bolker 2011). Commercial bushmeat hunting becomes economical on a large scale when existing infrastructure (largely logging roads) greatly reduces costs (Nasi *et al.* 2008). This is facilitated by the widespread use of motorcycles which can easily bypass barriers placed by logging companies at the junction of abandoned logging roads and permanent roads. However, we observed that following the closure of logging roads they were also abandoned by motorized poachers in <10 years. Hunters preferentially used currently open or recently abandoned logging roads rather than old ones which would require systematic removal of vegetation and fallen trees and repair of river crossings. Logging companies are trying to ban the transport of hunters, weapons and bushmeat in company vehicles and to set up guarded barriers at entry points to forest concessions (Poulsen, Clark & Bolker 2011). However, permanently open access roads, used and maintained by logging companies, do still allow hunters to reach an extensive network of footpaths (Clark *et al.* 2009). Stricter enforcement of existing hunting regulations might disrupt the relationship between logging companies and local people (Nasi *et al.* 2008) given the regionwide importance of bushmeat (Wilkie *et al.* 2000). However, if poaching is largely restricted to areas with current or recent logging activities, this means that the impact on wildlife occurs in limited areas in the wider forest landscape. After 10 years post-logging (one-third of a 30-year rotation), logging concession areas may act as refuges from hunting with an effectiveness similar to protected areas (Haurez *et al.* 2014). Abandoned logging roads can even attract endangered species such as gorillas that feed on the abundant *Aframomum* and Marantaceae herbs (Matthews & Matthews 2004). We therefore recommend further research on the long-term link between abandoned logging roads and wildlife populations.

CONCLUSIONS

Abandoned logging roads are transient intensively disturbed patches in the forest landscape in the Congo Basin, with a high level of resilience shown by the vegetation components of the rain forest ecosystem but with much slower recovery of biomass on road tracks than edges. Simple improvements to forest exploitation and restoration can reduce impacts and revalorize logged forests to enhance sustainable forest management (Fig. S7). These are as follows: (i) to reduce the amount of biomass removal and soil compaction, previous roads should be reopened for subsequent harvest operations; (ii) the clearing width for road construction should be reduced markedly. The resulting reduction of exposure to sunlight that allows the road surface to dry after rain should be compensated by improvements in road maintenance and drainage; and (iii) given the high capacity of road habitats for recruitment of commercial tree species, enrichment planting trials should be established in the edge zone of recent logging roads with and without removal of competing dominant herbs as long as the road track remains accessible. If successful, once mature these trees could be harvested with low cost and impact from the reopened road track.

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Data accessibility

Full inventories of vegetation and site characteristics are available from Dryad Digital Repository doi:10.5061/dryad.51p4f (Kleinschroth *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Data collection.

Fig. S1. Scatterplots of the main response variables against years after road abandonment.

Fig. S2. Mean values and 95% CI for four variables across substrate fertility classes.

Fig. S3. NMDS based on floristic dissimilarity across habitat zones and age classes.

Fig. S4. Genus-area accumulation curves for three road age classes.

Fig. S5. Scatterplots of environmental variables against years after road abandonment.

Fig. S6. Use of paths depending on time after road abandonment.

Fig. S7. Main conclusions and how they are linked.

Table S1. Mixed regression modelling results.

Tables S2. List of commercial species with density and frequency of observations.

Table S3. Area and AGB cleared for road construction across different concessions.

Table S4. Floristic dissimilarity between habitats and age classes.