Liana species decline in Congo basin contrasts with global patterns

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Abstract. Lianas, woody climbing plants, are increasing in many tropical forests, with cascading effects such as decreased forest productivity, carbon sequestration, and resilience. Possible causes are increasing forest fragmentation, CO_2 fertilization, and drought. Determining the primary changing species and their underlying vital rates help explain the liana trends. We monitored over 17,000 liana stems for 13 yr in 20 ha of old-growth forest in the Congo Basin, and here we report changes and vital rates for the community and for the 87 most abundant species. The total liana abundance declined from 15,007 lianas in 1994 to 11,090 in 2001 to 9,978 in 2007. Over half (52%) of the evaluated species have significantly declining populations, showing that the community response is not the result of changes in a few dominant species only. Species density change (i.e., the change in number of individuals per hectare) decreased with mortality rate, tended to increase with recruitment rate, but was independent of growth rate. Species change was independent of functional characteristics important for plant responses to fragmentation, CO_2, and drought, such as lifetime light requirements, climbing and dispersal mechanism, and leaf size. These results indicate that in Congo lianas do not show the reputed global liana increase, but rather a decline, and that elements of the reputed drivers underlying global liana change do not apply to this DR Congo forest. We suggest warfare in the Congo Basin to have decimated the elephant population, leading to less disturbance, forest closure, and declining liana numbers. Our results imply that, in this tropical forest, local causes (i.e., disturbance) override more global causes of liana change resulting in liana decline, which sharply contrasts with the liana increase observed elsewhere.

Key words: climbers; collapse; DR Congo; functional traits; Ituri; lianas; species abundance; tropical forest.

INTRODUCTION

Tropical forests appear increasingly dynamic over recent decades, with faster tree growth, mortality, and turnover (Phillips and Gentry 1994, Wright 2005, Lewis et al. 2009), and compositional changes in higher taxonomic levels (Laurance et al. 2004, Sande et al. 2016). Lianas (woody climbers) are increasing in number of stems, basal area, and biomass, especially in Neotropical forests (Phillips et al. 2002, Wright et al. 2004, Chave et al. 2008, Ingwell et al. 2010, Schnitzer and Bongers 2011, Schnitzer et al. 2012, Yorke et al. 2013, Laurance et al. 2014, Tymen et al. 2016). These changes have been attributed to more positive responses in lianas compared to trees to increases in atmospheric CO_2 concentrations (Lewis et al. 2009), fire-derived nutrient deposition (Hietz et al. 2011, Rozendaal and Zuidema 2011,

Schnitzer 2015), reduced rainfall (Swaine and Grace 2007), reduced cloud cover (Graham et al. 2003), increased forest disturbance and tree turnover rates (Laurance et al. 2001, Phillips et al. 2002), and increased frugivore removal by hunters, which has less effect on more wind-dispersed lianas (Wright et al. 2007). Lianas are thought to respond quickly to increasing CO_2 concentrations and N deposition because of their fast inherent growth rates, and to increasing disturbance rates because of their high light requirements (Laurance et al. 2001). Lianas are important components of tropical forests, comprising between 15% and 45% of the woody individuals and species (Gentry 1992, Schnitzer and Bongers 2002, Schnitzer 2005) and contributing up to 40% of forest leaf area and leaf production (Wright et al. 2004). Increases in liana abundance inhibit tree growth and abundance (Peña-Claros et al. 2008, Visser et al. 2018) and result in decreased ecosystem productivity and carbon storage. The increase may cascade into changed communities of pollinators, herbivores, and symbiotic fungi, some of which are highly species specialized.

The recent increases of lianas in tropical forests (Schnitzer and Bongers 2011, Schnitzer 2015) are based on stand-level changes in liana density (Phillips et al. 2002), or inferred from leaf litter production (Wright et al. 2004, Wright and Calderón 2006) or tree infestation levels (van der Heijden and Phillips 2009, Ingwell et al. 2010, Toledo et al. 2011, Wright et al. 2015, Visser et al. 2018), and consequently may be driven by a few dominant species (cf. Katabuchi et al. 2017). However, understanding the ecological causes of liana change requires evaluating the underlying demographic processes, and how species-specific responses are associated with species characteristics and changes in the environment that shape these responses. Environmental causes of change include increased light levels due to disturbance (*disturbance-hypothesis*; Putz 1984, Schnitzer and Bongers 2002, 2011; leading to higher recruitment and faster growth of light-demanding liana species), increased nutrient deposition and atmospheric carbon dioxide levels (*fertilization-hypothesis*, Phillips et al. 2002; leading to liana increase accompanied by increased growth), increased drought (*dry-season-growth-advantage-hypothesis*, Schnitzer 2005; leading to an advantage of lianas compared to trees), or a combination of these. So far, none of the earlier studies showed demographic changes at the species level, and these studies can therefore not rule out that the community changes are driven by one or a few dominant species.

We monitored all liana stems in 20 ha of old-growth forest in the Congo Basin for a 13-yr period. With 2 million km^2, the Congo Basin is the second largest remaining area of tropical forest in the world. We examined population trends of all liana species together and related these to underlying vital rates (recruitment, growth, mortality). We also focus on population trends of the 87 most dominant species, and relate these to the underlying species vital rates and to the species functional traits. This study is the first that evaluates old-growth forest species-level demographic rates for such a large number of liana species, and is unique in covering such a long time scale.

METHODS

Study area and data collection

Research was carried out in the Okapi Faunal Reserve (1°25′ N, 28°35′ E), north-eastern DR Congo. Mean annual precipitation is 1,785 mm with a 3-month dry season (<100 mm/month) and mean annual temperature between 17.9°C and 25.5°C. Altitude varies between 700 and 850 m above sea level (asl), and most of the soils are highly weathered oxisols. Vegetation in the area has been classified as mixed tropical lowland forest (sensu White 1983), with a 30–40-m-tall canopy (see also Hart 1985, Makana et al. 2004, Ewango 2010, Bongers and Ewango 2015, Ewango et al. 2015). Two 10-ha permanent forest plots were established in old-growth mixed forest in 1994 and were recensused in 2001 and 2007. All lianas ≥2-cm diameter at breast height (DBH) were tagged, mapped, identified, and measured for their DBH, following a standard protocol (Gerwing et al. 2006). If there were stem irregularities the diameter was measured at the nearest height where the stem was cylindrical. At each recensus, it was checked whether individuals were alive or dead, the diameter of alive individuals was measured, and newly recruited individuals were recorded.

Population change, vital rates, and functional traits

We calculated liana stem density and basal area for the three censuses (1994–2001–2007), both directly from the data, as well as using a bootstrapping procedure (see below). We selected the 87 most abundant species (i.e., 35.5% of all species and 95% of all stems) that had at least 15 stems in one of the three censuses (Appendix S1: Table S1). All liana and species-specific changes in number of individuals, recruitment and mortality rates, and annual diameter growth rates were calculated for the period 1994–2001, 2001–2007 and for the whole period 1994–2007 (following Sheil and May 1996 and Sheil et al. 2000). We excluded species that had fewer than seven surviving individuals in the respective census interval. For the 1994–2001 interval, 85 species remained, for the 2001–2007 interval 81 species remained, and for the full (1994–2007) interval 80 species remained. To examine temporal changes in population density per species we calculated density change (DC): the ratio of abundance at end of period (N_2) over abundance at the beginning (N_1). DC > 1 indicates a population increase, DC < 1 a population decrease, and DC = 1 indicates a constant population size. To be able to compare increases and decreases we natural log transformed DC into lnDC (e.g., 0.5 and 2 have the same deviation from 1), and a lnDC of zero indicates a ratio of 1, and hence, no change. Per surviving individual for the two short and the full time period, absolute annual diameter growth rates (in mm/yr) were calculated as $(DBH_2 − DBH_1)/(t_2 − t_1)$, where DBH refers to the diameter of the individual, and t to time of the final and initial census (in years), respectively. All liana and species-level diameter growth values were calculated by averaging across all individuals of all species together and per species. Annual mortality rate (M, in %/yr) was calculated as $M = 100 × [1 − [1 − ((N_0 − N_t)/N_0)]$**$1/t]$, in which N_0 refers to the number of individuals at the start of the period, N_t to those surviving till the end, and t is the interval period in years. Annual recruitment rate (R, in %/yr) was calculated as $R = 100 × [1 − [1 − (N_r/N_t)]$**$1/t]$, where N_r is the number of recruits between beginning and end of the measuring period. The time interval was defined as the arithmetic mean time between censuses for individuals of that species, based on the census data of each $20 × 20$ m subplot in the plots.

To evaluate if species performance is related to species traits, we used four performance-related functional traits that are important for responses to disturbance, drought, and CO_2 fertilization: dispersal syndrome, climbing mechanism, leaf size, and light requirements. Dispersal syndrome (animal-dispersed: zoochory, explosive: barochory, and wind-dispersed: anemochory) is an indicator of the potential dispersal distance (increasing distance from baro-, through anemo- to zoochory). The climbing mechanism (hook, tendril, twiner, and root) indicates how quickly and with what investment species access the canopy. Leaf size (small: ≤ 20 cm^2 or large: >20 cm^2) is important for light capture, regulation of the heat balance of the plant and responses to drought. Finally, lifetime light requirements (light demanding vs. shade tolerant) indicate whether species need disturbances for the completion of their life cycle. Trait data were compiled based on the literature (Evrard 1968, Bongers et al. 2005, Jongkind 2005) and field observations for the 72 species that were identified to species level.

Statistical analyses

We estimated the confidence limits for density and basal area of the whole liana community, and for recruitment, mortality, and diameter growth of the whole liana community and per species using a bootstrapping approach. Five hundred 20 × 20 m plots were drawn randomly from the 20 ha, with replacement. After the draw, community density and basal area were calculated for each census, summed over the 500 20 × 20 m subplots, and scaled per hectare. Annual recruitment and mortality rates were calculated across all individuals in the 500 subplots for the three census periods, and annual diameter growth rates were calculated for all surviving individuals in the 500 subplots, and averaged across all individuals for the three census periods. Similarly, recruitment and mortality rates were calculated per species. This was done 1,000 times and we calculated medians using the 500th highest value, and the 95% confidence intervals using the 25th highest value as lower confidence limit and the 975th highest values as upper confidence limit. This way, we determined the confidence intervals without assuming a normal distribution, and avoided negative confidence intervals for recruitment and mortality. Nonoverlapping confidence intervals then show differences between the three censuses in community basal area and tree density, and differences between the census intervals in community and species recruitment, growth and diameter growth. For lnDC, the species or liana community has significantly changed in abundance when this confidence interval does not include 0. For diameter growth in the two short census intervals and in the full census interval, we calculated the mean and 95% confidence intervals based on all individuals per species. For further analyses on species-level lnDC,

recruitment and mortality, we used the bootstrapped median value per species.

Weighted Pearson correlation analyses were used to test how species-level lnDC, recruitment, mortality, and DBH growth rate were correlated between the observation periods. We weighted species by their ln-transformed average abundance across the three census years, in order to incorporate differences among species in the precision of the estimate of the mean and their contribution to total community changes. To test the effect of recruitment, mortality, and growth rate on lnDC, we used three linear models, also with the ln-transformed average abundance per species as weights. To test if lnDC, recruitment, mortality, and diameter growth were affected by functional species characteristics, we used analysis of variance (ANOVA) per response variable (e.g., lnDC) and trait (e.g., dispersal syndrome), and weighted species by their ln-transformed average abundance across census years. In case the trait effect was significant and the trait had more than two levels (i.e., for dispersal syndrome and climbing mechanism), we evaluated pairwise differences using pairwise t tests. Prior to correlation analyses, regression analyses and ANOVAs, we ln-transformed recruitment, mortality, and diameter growth. All statistical analyses were performed using R version 3.5.1 (R Foundation for Statistical Computing, Vienna, Austria). The correlation analyses were performed using the *wtd.cor* function from the *weights* package, linear models with the *lm* function, ANOVAs using the *Anova* function using the *car* package, and the pairwise t tests using the *pairwise.t.test* function in R.

Results

Overall, liana stems declined dramatically over the 13-yr period, from 15,007 in 1994 through 11,090 in 2001 to 9,978 stems in 2007 (which is 750–555–499 stems/ha), and a basal area change from 16.18 in 1994 through 15.19 in 2001 to 14.69 m^2 in 2007 (which is 0.809–0.759–0.735 m^2/ha; Fig. 1; Appendix S1: Table S2). Confidence intervals resulting from bootstrapping showed that the changes in density were significant, but the changes in basal area were not (although between 1994 and 2007 the overlap in confidence limits was minimal). Density change was consistently negative and was stronger the first period compared to the second (Appendix S1: Table S2). The underlying vital rates for all lianas combined showed an increasing recruitment rate (with only slightly overlapping confidence intervals between the two periods) but a clearly significant decreasing mortality rate and diameter growth rate (in both cases higher in the first period).

Out of the 87 liana species analyzed, 58 species changed significantly in stem density (Fig. 2): 52% decreased and 15% increased, and the remaining species did not change significantly. The population change over the 13 yr was calculated as the ratio of final density over initial
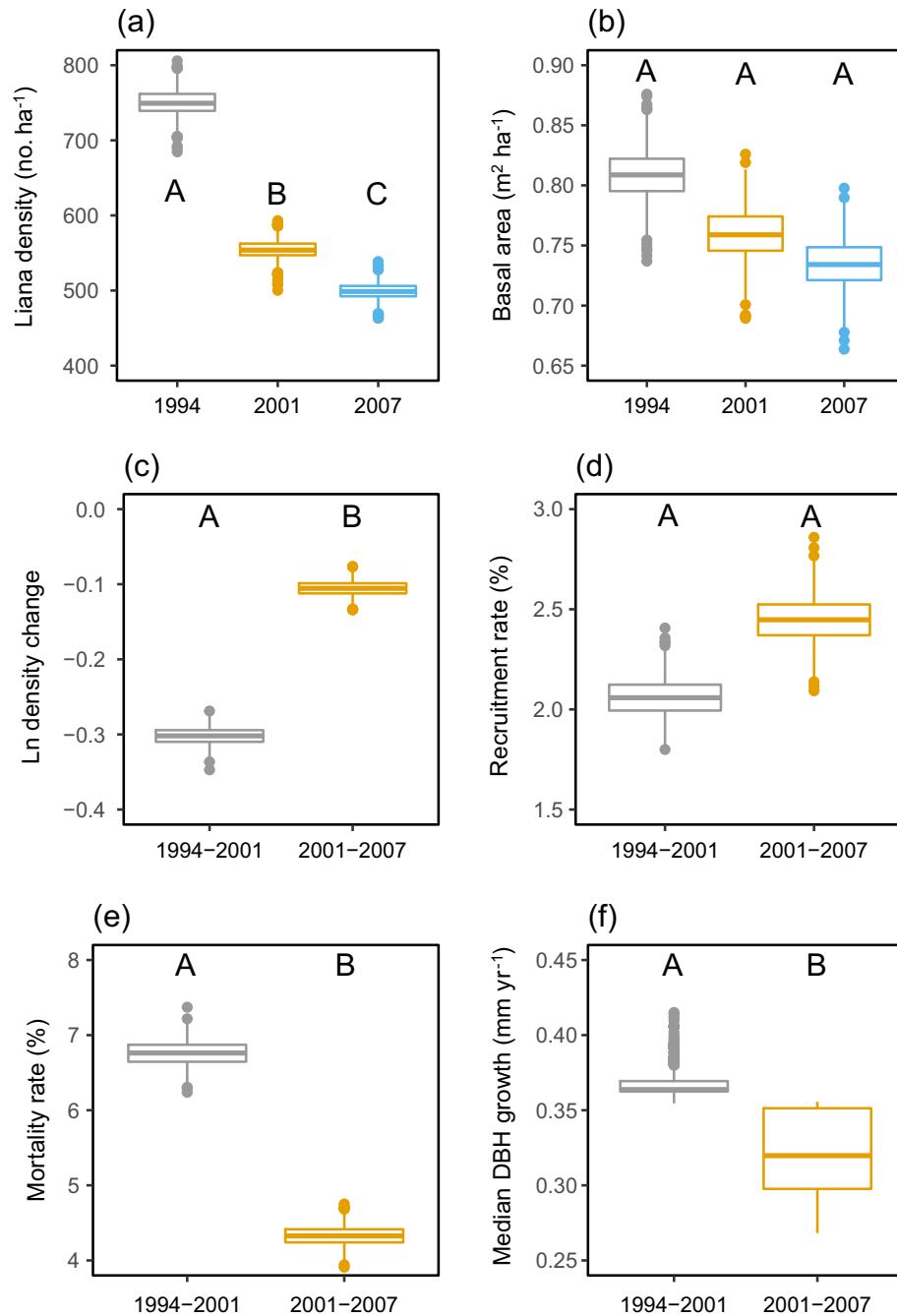
Fig. 1. Changes in total liana abundance and vital rates in 20 ha of mixed Ituri forest, DR Congo. (a) Stem density and (b) basal area per hectare in each of three censuses (1994, 2001, and 2007), and (c) ln density change, (d) recruitment rate, (e) mortality rate, and (f) diameter growth rate during the two census periods. All boxplots are based on bootstraps, and show the medians, confidence intervals (2.5% and 97.5%), and outliers values from the bootstraps.

density (lnDC, density change). lnDC ranged from −3.61 for the collapsing *Manniophyton fulvum* Mull.Arg. (Euphorbiaceae) to 2.19 for the increasing *Adenia lobata* (Jacq.)Engl. (Passifloraceae). A change in population density is the net change of recruitment and mortality. Per-species recruitment rates averaged $12.5 \pm 29.8\%$ (mean $\pm$ SD) per year; mortality rates averaged

14.1 ± 30.0 (Appendix S1: Table S1). Species growth averaged 0.62 ± 0.52 mm (mean $\pm$ SD) per year (Appendix S1: Table S1). Initial population size per species affected final population size ($r = 0.85$, $P < 0.001$) and lnDC ($r = -0.35$, $P = 0.001$), but was not related to recruitment rate ($r = -0.09$, $P = 0.393$) or mortality rate ($r = 0.06$, $P = 0.585$) (Appendix S2: Fig. S2).

Species lnDC, recruitment and mortality rates, and growth were consistent over the two periods, with significant correlations between the first and the second period (lnDC: Pearson $r = 0.35$, $P < 0.001$; recruitment: $r = 0.42$, $P < 0.001$; mortality: $r = 0.65$, $P < 0.001$; growth: $r = 0.72$, $P < 0.001$, Appendix S2: Fig. S3). Density change (lnDC) decreased with mortality (slope $= -0.93$, $P < 0.001$), tended to increase with recruitment rate (slope $= 0.23$, $P = 0.065$, but without *Manniophyton fulvum* slope $= 0.36$, $P < 0.001$), and was independent of growth rate (slope $= 0.18$, $P = 0.645$; Fig. 3a–c). Recruitment rate and mortality rate were unrelated ($r = 0.05$, $P = 0.648$), and so were recruitment rate and DBH growth ($r = 0.21$; $P = 0.064$) and mortality rate and DBH growth ($r = 0.04$; $P = 0.703$; Fig. 3d–f).

Light demand, climbing strategy, dispersal syndrome, or leaf size did not significantly affect density changes over time (Fig. 4, P values 0.76–0.87–0.82–0.10, respectively). Recruitment rate differed among climbing strategies and dispersal strategies, mortality rates differed among climbing strategies and between leaf sizes, and diameter growth differed among climbing, dispersal, and light requirement strategies (Appendix S2: Fig. S4).

Discussion

We found a significant decrease in lianas abundance over the 13-yr time period in Ituri forest. This decrease is in line with the overall liana decline in the two other African forests evaluated (Caballé and Martin 2001, Thomas et al. 2015) but contrasts with the general increase of lianas in the Neotropics (Phillips et al. 2002, Schnitzer and Bongers 2011, Laurance et al. 2014, Schnitzer 2015, Ceballos and Malizia 2017, Hogan et al. 2017; but see Smith et al. 2017, Geralomo et al. 2018) and an increase (Pandian and Parthasarathy 2015) and a relatively stable population (Wright et al. 2015) in Asia.

Our study is one of the first to evaluate individual species changes for more than a few liana species (Caballé and Martin 2001, Nabe-Nielsen 2002, but see Londre and Schnitzer 2006, Hogan et al. 2017). We found pervasive changes in the liana species population densities, but in contrast to expectations, population densities of most species declined rather than increased. Liana species population densities decreased with increasing mortality rate, as expected, and tended to increase with recruitment rate.

Lianas are thought to be more responsive than trees to changing light conditions (Putz 1984, Schnitzer and Bongers 2002), and may take faster advantage of fertilization with increased carbon dioxide (Chave et al. 2008, Körner 2009, Lewis et al. 2009) and nutrients (Chen et al. 2008).

The observed patterns in vital rates indicate that elements of the main hypotheses underlying global liana increase are rejected in our study. Every hypothesis consists of an environmental change (which can be in two directions—increase or decrease), and a part of a liana response to that change. The *disturbance-hypothesis* (Putz 1984, Schnitzer and Bongers 2002, 2011) states that increased forest disturbance opening up the forest leads to more light (the environmental change part) and therefore higher recruitment and faster growth of (light-demanding) liana species (the response part). We did not find such overall liana increases. Instead we found that, overall, lianas decreased over the observation period. As the forest has been closing over the evaluated period (see below) the changes we observed may be responses to a disturbance decrease rather than a disturbance increase. The *fertilization-hypothesis* (Phillips et al. 2002) states that increasing CO_2 and N depositions likely lead to high fertilization (the environmental change part) to which lianas respond quickly with rapid growth and reproduction, resulting in overall increased liana abundance (the response part). In our forest most liana species were decreasing, and lnDC was independent of growth rate. Fertilization may be too low in this forest region (cf. for nitrogen, Hietz et al. 2011). It is also possibly that the liana species do not respond quickly enough. The *dry-season-growth-advantage hypothesis* (Schnitzer 2005) predicts increased droughts (the environmental change part) to which lianas would respond favorably, as lianas increase (DeWalt et al. 2010, Toledo et al. 2011) under changes in rainfall patterns and increasing El Niño droughts (Holmgren et al. 2001, Condit et al. 2004). The Ituri forest area did not experience strong drought effects during the last two decades, despite decreasing rainfall (Asefi-Najafabady and Saatchi 2013, Zhou et al. 2014), and species with small-sized leaves (an indicator of drought tolerance) did not differ from species with large-sized leaves in their lnDC. Climate modelers found no change in drought risk (Otto et al. 2013) and future climate model projections indicate rainfall increase in this area (James et al. 2013), although concordance among models is weak and more ground-based data to improve model prediction accuracy are needed (Washington et al. 2013). Thus, if the increased drought is not occurring we should not expect lianas to increase. Our data are thus inconclusive towards this hypothesis.

Species-level density changes were not affected by the species' functional traits: climbing strategy, dispersal mode, leaf size, and lifetime light requirement. Recruitment rate was only affected by climbing and dispersal strategies. We had expected lifetime light requirement to affect all population change trends, but it only affected diameter growth. Most of the studied species and individuals were light demanders (83% of our 72 identified abundant liana species in 1994, 80% of the studied individuals). This is in line with the generally open structure of the Ituri forest (average canopy cover of 20×20 m subplots was only 58.5%; data not shown), which may partly be a result of the many forest elephants that were inhabiting this area until recently. The pervasive liana changes and the massive decline of the strongly dominant species that we observed are most likely due to
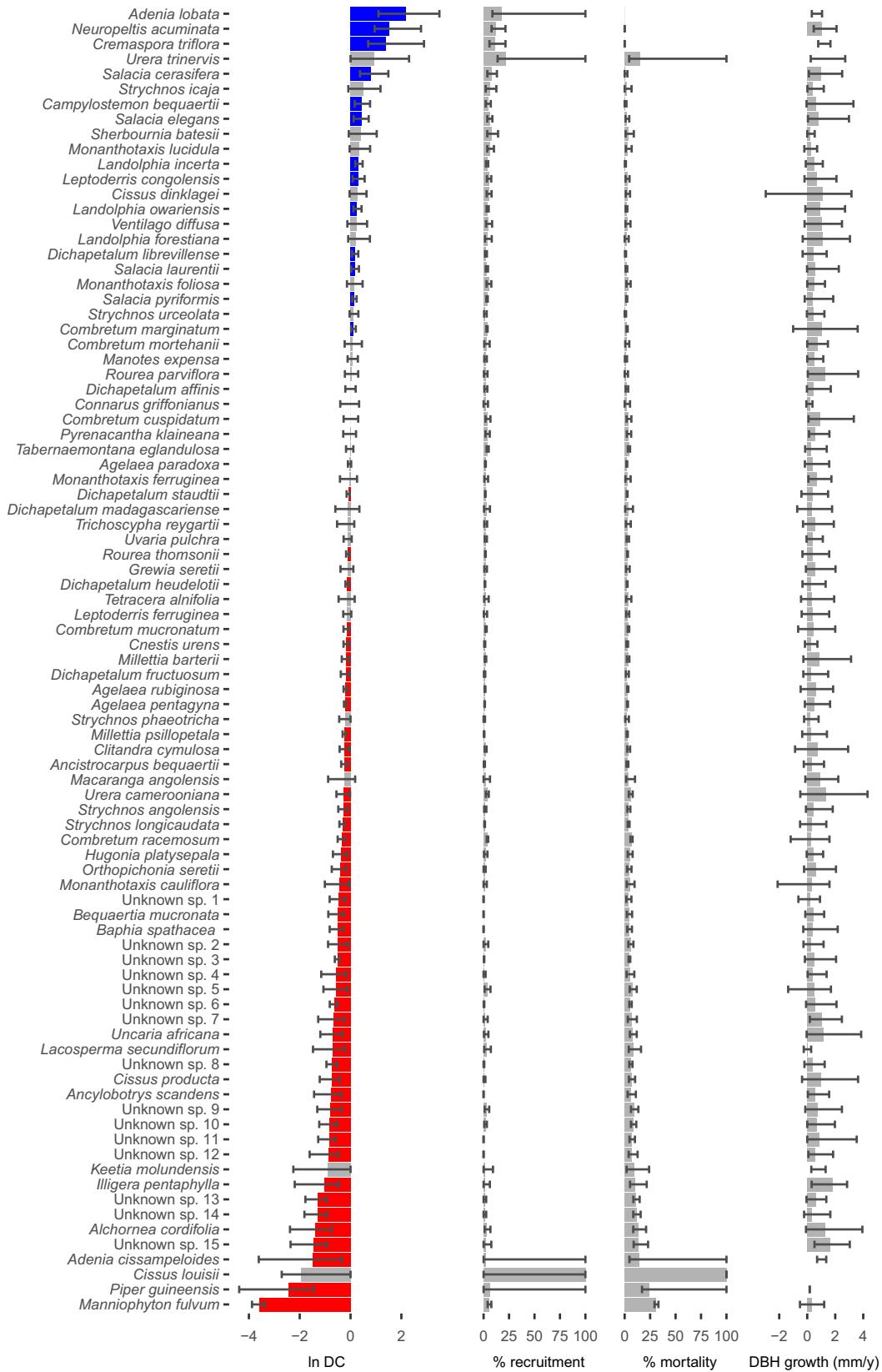
FIG. 2. Density changes, recruitment, mortality, and diameter growth rates of 87 liana species over a 13-yr period in Ituri forest,

(Fig. 2. *Continued*)

DR Congo. Each bar represents a different species (medians with confidence intervals for all except growth rates, which represents means with confidence intervals). Density change is here presented as the natural logarithm of the ratio of density in 2007 over the density in 1994 to make positive and negative deviations from equity (DC = 1) comparable. Species density changes range from strongly negative (decreasing between 1994 and 2007) to positive (increasing species). Significances are based on the 95% confidence intervals of the bootstraps (see *Methods*) with red bars indicating species showing a significant decrease, gray bars indicating no change, and blue bars indicating species showing a significant increase. Underlying data are given in Appendix S1: Table S1.

local rather than global drivers. Locally, more cloudy weather and thus a reduced irradiance can limit net CO_2 uptake and growth of rainforest trees (Graham et al. 2003), and is expected to inhibit light-demanding lianas. Probably more importantly, the Ituri forest may be recovering from past disturbances, as many other African forests (van Gemerden et al. 2003, Willis et al. 2004, Brncic et al. 2007, Lewis et al. 2009). The increased poaching (Effiom et al. 2013) and the strong reduction in forest elephants (Beyers et al. 2011, Poulsen et al. 2017) is leading to less browsing and damage and a closing forest (C. E. N. Ewango, *personal observation*). This may have led to a reduction of lianas, especially the most light-demanding species. Over the 13 yr, the total number of light-demanding individuals of the selected 72 species decreased by 40%, whereas the shade-tolerant individuals decreased

only 8%. With these 72 species covering 87% of all individuals in both 1994 and 2007, we are confident that this reflects the overall liana community. For our forest we show that indeed the whole community changes are similar to the changes in a large number of species, and do not reflect just a few dominant ones. This is not always the case, however. Katabuchi et al. (2017) showed that just a few species (1–6 out of 312) were responsible for the community-level changes in functional composition. We predict the light-demanding species to decrease further with continued development towards a more closed old-growth forest, as has been shown for Ugandan forests (Sheil et al. 2000, Sheil 2001). We postulate, therefore, the *recovery-from-past-disturbances hypothesis* to be the most probable explanation for the pervasive decline in liana species in this Congo Basin forest.
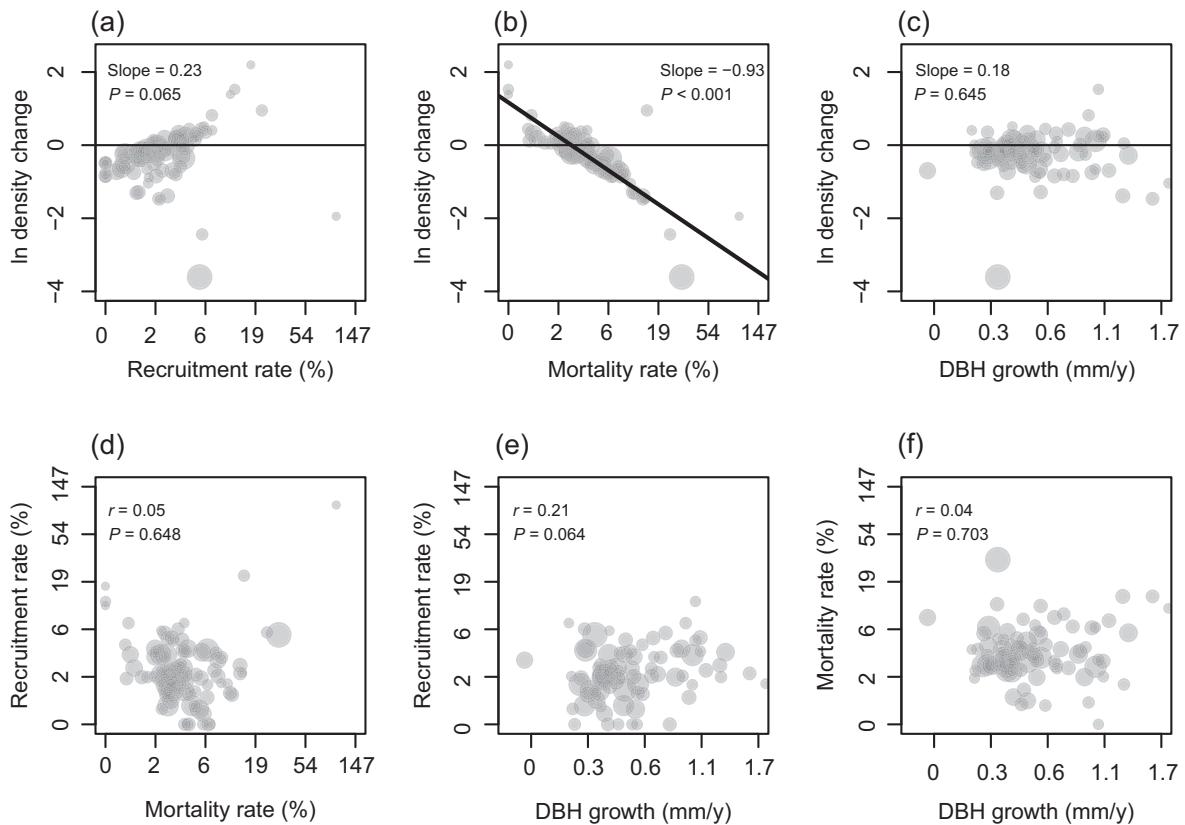

Fig. 3. Relationship between density change (lnDC) and (a) recruitment rate, (b) mortality rate, and (c) diameter at breast height (DBH) growth for 87 liana species, and correlations across (d) recruitment rate, (e) mortality rate, and (f) DBH growth rate for 80 or more species over a 13-yr period in Ituri forest, DR Congo. Rates are per year. The horizontal line indicates zero density change. The size of the points is scaled to the ln-transformed mean species abundance. Note that the upper three graphs are based on regression results, and significant relationships are indicated by a continuous line, whereas the lower three graphs are based on correlation results, and no trend lines are added.
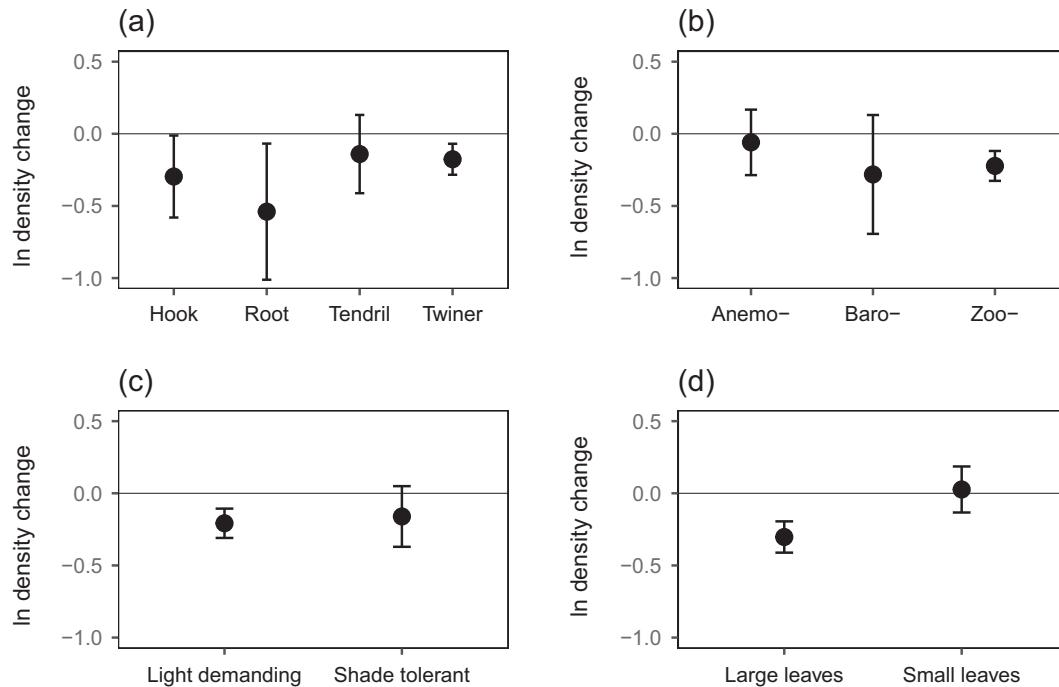
Fig. 4. Comparisons of density change between species groups based on performance-related functional traits. We selected climbing mechanism (hook, root, tendril, twiner), dispersal syndrome (wind-dispersed: anemochory, explosive: barochory, and animal-dispersed: zoochory), light requirements (light demanding vs. shade tolerant), and leaf size (large leaf: >20 cm^2 or small leaf: ≤ 20 cm^2). Points indicate means with standard error, as derived from the linear model with species weighted by their ln-transformed average abundance. The horizontal line indicates no density change. For species classifications see Appendix S1: Table S1. None of the species groups differed significantly (ANOVA tests; climbing mechanism $F = 0.24$, $P = 0.87$; dispersal syndrome $F = 0.24$, $P = 0.79$; light requirement $F = 0.04$, $P = 0.84$; leaf size $F = 2.91$, $P = 0.09$).

Of our 72 identified liana species, 79% is animal-dispersed, and dispersal strategy significantly impacted recruitment and growth rates of species. Increased hunting was suggested to favor wind-dispersed over animal-dispersed species (Wright et al. 2007), possibly partly explaining the Neotropical increase in lianas, which were mostly wind-dispersed. In many other (tropical) forests with high hunting pressure (including African), lianas are mainly animal-dispersed (Wright et al. 2015), which would lead to a decline in their abundance.

Our results support the diversifying patterns of liana changes in tropical forests. We conclude that in some forests local phenomena, in this case the elephant-mediated disturbance, override the more global drivers of liana change.

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