## Forest Ecology and Management 369 (2016) 155-160



# Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Effects of reduced-impact selective logging on palm regeneration in Belize



<sup>a</sup> Friends for Conservation Development, Chi-Ha Street, San Jose Succotz, Cayo District, Belize

<sup>b</sup> University of Belize, Faculty of Science and Technology, Department of Biology, Belmopan, Belize

<sup>c</sup> University of Belize Environmental Research Institute, Price Centre Road, Belmopan, Belize

<sup>d</sup> The Forestland Group, Chapel Hill, NC 27514, USA

<sup>e</sup> Department of Biology, University of Florida, Gainesville, FL 32611-8526, USA

#### ARTICLE INFO

Article history: Received 23 December 2015 Received in revised form 17 March 2016 Accepted 18 March 2016 Available online 26 March 2016

Keywords: Arecaceae Biodiversity Forest disturbance Forest management Tropical silviculture

#### ABSTRACT

To assess the impacts of a low-intensity selective timber harvest on a palm community in Belize, we mapped logging infrastructure (i.e., roads, log landings, skid trails, and stumps) and measured palm regeneration 1 year after a timber harvest carried out using reduced-impact logging (RIL) practices. We sampled palms across a gradient of increasing harvest impact severity from areas not directly affected by logging, in felling gaps, on secondary and primary skid trails, and on log landings. We used generalised linear mixed-effect models fitted in a Bayesian framework and applied a non-metric multi-dimensional scaling of the ecological distances between sites to evaluate differences in palm seedling regeneration density and species composition, respectively. The harvest of an average of 2.5 trees ha<sup>-1</sup> caused 0.4% of the forest to be converted to log landings, 0.7% and 3.6% to roads and skid trails, and 2.3% to felling gaps, which left 93.0% of the 350 ha harvest block with no direct impacts of logging. The difference in abundance and species composition of palm regeneration in unlogged areas compared to felling gaps and skid trails was small, but log landings had markedly lower densities. These results highlight that the impacts of selective logging are minor at least where harvest intensities are low and RIL practices are employed. If further reductions in canopy opening and soil disturbance are desired, we recommend that logs be cable-yarded (i.e., winched) the final 20 m to skid trails instead of driving to the tree stumps. We estimate that implementation of this practice would reduce total skid trail coverage from 3.6% to 2.9% and overall forest disturbance from 7.0% to 6.3%. However, further reductions in disturbance might be inimical to the maintenance of palms and will certainly not favour regeneration of light-demanding commercial timber species (e.g., Swietenia macrophylla).

© 2016 Elsevier B.V. All rights reserved.

# 1. Introduction

Published assessments of the impacts of selective logging on tropical forests mostly focus on invertebrate and vertebrate species (e.g., Berry et al., 2010; Burivalova et al., 2014), with fewer studies on plants (but see Cannon et al., 1998; Duah-Gyamfi et al., 2014; de Avila et al., 2015) and fewer yet where reduced-impact logging (RIL) practices were employed (but see Bicknell et al., 2014). To help sustain timber yields, minimize carbon emissions, and reduce adverse impacts on biodiversity, RIL methods are advocated for selective logging of tropical forests (Putz et al., 2008). Given that

\* Corresponding author. *E-mail address:* aroopsind@ufl.edu (A. Roopsind). RIL and other silvicultural interventions unavoidably and purposefully change forest structure and composition, it is important to document the responses of plant taxa not directly targeted for extraction. Here we focus on the impacts of RIL on palms (Arecaceae) across a gradient of micro-environmental conditions created by selective logging in a lowland tropical forest in Belize.

Palms are geographically widespread, ecologically diverse, and often critical for the maintenance of ecosystem functions, wildlife populations, and local livelihoods (e.g., Balick and Beck, 1990; Goodman et al., 2013). Furthermore, palm resilience to disturbance is well documented for fire-maintained ecosystems (Abrahamson, 1999; Anderson et al., 1991), but not for logged forests. Palms may also be disproportionately prone to damage during selective logging operations given their lack of both taproots and large





diameter structural roots; these characteristics render them easy to topple and hence are often not avoided when roads and skid trails are opened. Palms that have emerged from the establishment growth phase and have their apical meristem above the ground are killed if pushed over (Henderson and Tomlinson, 1991); if palmrich areas are preferred by heavy equipment operators, infrastructure installation may reduce recruitment by killing reproductively mature individuals (Darrigo et al., 2016). In contrast, palms that are still in the establishment growth phase during which their apical meristem is below-ground generally survive trampling, mowing, burning, or any other activity that kills their above-ground parts (note that stilt-rooted palms do not pass through an establishment growth phase and hence lack the capacity to re-sprout after being top-killed). Given the potential susceptibility of large palms and resilience of small ones, it is not clear how palms fare in areas subjected to selective logging.

In this study we mapped and measured the effects of lowintensity selective RIL on forest structure and palm regeneration in Belize. We categorized disturbances by intensity of surface soil disruption (i.e., compaction and movement by heavy equipment) and changes in understory light conditions. We expected that higher intensities of disturbance favours palms over other plant growth forms because palms tolerate compacted soils (Emilio et al., 2014) and, as seedlings, they readily recover from aboveground disturbances. At the same time, we also expected that low intensity RIL impacts would, overall, be restricted in their distribution and therefore have minimal impacts on palm regeneration (Schwartz et al., 2014). By assessing both the spatial extent of forest management activities and their impacts on palm regeneration in a hurricane-prone forest, we explore the response of the most abundant plant family in the neotropics (ter Steege et al., 2013) to low-intensity selective logging.

# 2. Methods

#### 2.1. Site description

The study was conducted on the 42,301 ha Laguna Seca property of the Yalbac Ranch and Cattle Corporation in Orange Walk District, Belize (17°15′N, 89°04′W). The area is characterized by lowland, broad-leaved, moist forest on gently rolling karstic topography (~88 m asl) with shallow soils over limestone. The annual average precipitation is  $\sim$ 1400 mm, with a pronounced dry season from February to May. Over the past 5000 years, hurricanes made landfall in central Belize about once per decade (McCloskey and Keller, 2009), but with increased sea surface temperatures, hurricane frequencies and intensities are expected to increase (Knutson et al., 2010). Deforestation rates in Belize between 1980 and 2010 averaged only 0.61% per year, (9650 ha year<sup>-1</sup>; Cherrington et al., 2010), but this rate recently increased substantially due to deforestation for industrial agriculture (Cherrington et al., 2012) and includes a clearing in excess of 10,000 ha immediately adjacent to the studied forest (personal observation, all authors).

This Forest Stewardship Council (FSC) certified forest is managed under a long-term license that permits selective logging with RIL practices on a 40-year rotation. Commercial trees 45–90 cm DBH (stem diameter at 1.3 m) are harvested at an average intensity of 2.7 trees ha<sup>-1</sup> (2.9 m<sup>3</sup> ha<sup>-1</sup>). The principal harvested species are *Swietenia macrophylla* (mahogany), *Calophyllum brasiliense rekoi* (Santa Maria), *Manilkara zapote* (sapodilla), and *Lonchocarpus castilloi* (cabbage bark). Palms present in the study area include the subcanopy (up to 10–20 m tall) species *Cryosophila stauracantha, Sabal mauritiiformis, Guassia maya* and *Attalea cohune*, two understorey species (*Bactris mexicana* and *Chamaedorea oblongata*), and one liana (*Desmoncus orthacanthus*; all species hereafter referred to by their generic names).

#### 2.2. Data collection and analysis

Data were collected in March 2015 in a 350 ha area that was logged in February-May 2014. Palm seedlings (i.e. individuals with no above-ground stem and leaves <1 m long; no fully stilt-rooted species occur in the study area) were counted in randomly located  $2 \times 20$  m plots across a five-class gradient of disturbance severity in 11 separate harvest areas. In each of the 11 areas we sampled a log landing, a primary skid trail used to yard  $\ge 2 \log s$ , a secondary skid trail used to yard only one log, a felling gap, and an area of undisturbed forest within the logged area hereafter referred to as 'not affected directly area' (NADA). The average distance between the 11 harvest areas was 800-1000 m, with log landings used as our point of access to the other logging disturbance categories. Skid-trail plots were parallel with and in the centres of skid trails at random locations. NADA plots were randomly located at distances of 25-35 m from the edge of the nearest skid trail or logging gap. Palm seedling data were collected within the  $40 \text{ m}^2$  plots, while non-palm woody plant seedlings (<1 m tall), which were much more abundant, were subsampled in five circular 1 m radius subplots located at 5 m intervals along the central axis of each main plot. Relative abundance of palm regeneration was calculated as the sum of all palm seedlings across species relative to the total woody plant regeneration (palm and non-palm woody seedlings). Percent canopy cover was measured at 1 m above the ground with a spherical densiometer (Lemmon, 1956) at 5 and 15 m along each of these transects.

We used the rstanarm package (Gabry and Goodrich, 2016) in R (R CORE TEAM, 2010) to fit generalized linear mixed-effects models in a Bayesian framework to quantify the effects of logging on the abundance of palm regeneration. The model results presented were fitted with a negative binomial distribution to account for the large proportion of zeros in the dataset. Palm species were treated as random effects and logging disturbance as fixed effects. Models with random intercepts and slopes for species across disturbance categories did not converge and were discarded. We report the mean and 95% credible intervals for the effect size of different logging disturbances based on draws from our posterior distribution.

We also estimate the ecological distance between all pairs of plots using the Bray–Curtis method for the species-specific palm abundance data, ignoring non-palm woody regeneration. We apply a non-metric multidimensional scaling (NMDS) to display the rank-order of distances between sites in a two-dimensional unconstrained ordination space. We included a weighted average species score on the ordination plot to allow for interpretation that sites closer to a species would be expected to have high abundance of that species, whereas sites that are farther away are expected to have lower abundance. We preformed these analysis with the Vegan package in R (Oksanen et al., 2010).

We extrapolate our plot level data on the impacts of logging on palm seedling density to the entire 350 ha 2014 logging area in which the locations of all log landings, roads, skid trails, and felled tree gaps were mapped with a GPS. We used the average areas of log landings ( $1225 \text{ m}^2$ ) and felling gaps ( $90 \text{ m}^2$ ) along with the average widths of roads (7 m) and skid trails (3.4 m) to calculate the proportion of the forest directly affected by logging and to portray those changes on a stylized map of 25 ha (Fig. 1). The map represents actual roads, skid trails, and log landings, as well as the spatial locations of all harvested trees. To visualize the felling gaps, we assigned at random to each tree stump mapped one of the 31 felling gaps we measured and mapped in the field.



**Fig. 1.** A 25-ha portion of block 40C of the Laguna Seca management unit logged in 2014. The map depicts NADA (not directly affected area; dark green), primary and secondary skid trails (white and light green lines, respectively), secondary logging road (highlighted line), felling gaps (light green), and a log landing (white) represented as mean dimensions based on samples from the same logging area; felling gaps, which differ in size and shape, were selected at random from 31 measured gaps and do not represent the actual gaps in the illustrated area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 3. Results

The 350 ha study site, which was the entire logging coupe for 2014, contained 11 log landings, 3.5 km of roads, 37.2 km of skid trails and 994 felling gaps. In terms of the proportion of the 350 ha logged area, skid trails accounted for the most disturbance (3.6%), felling gaps covered 2.3%, roads covered 0.7%, and log landings covered only 0.4% for a total area directly affected by logging of 7.0%. Canopy densiometer measurements showed that NADA had the highest canopy cover (97.4% SE 0.40) followed by primary skid trails (89.0% SE 0.97), secondary skid trails (87.4% SE 2.86), felling gaps (79.4% SE 3.0), and log landings (12.8% SE 1.67).

In the 55 40 m<sup>2</sup> plots we recorded 3259 palm seedlings representing six species with *Cryosophila* the most common (2322), followed by *Sabal* (540), *Chamedorea* (246), *Desmoncus* (70), *Bactris* (67), and *Guassia* (14); *Attalea* was not present in the plots. Model predictions for species-specific baseline regeneration across disturbances matched observed species abundances with *Cryosophila* accounting for the majority of regeneration (Fig. 3).

Palm regeneration densities across species (stems ha<sup>-1</sup>) in NADA, felling gaps, secondary skid trails, primary skid trails, and log landings were 858.3 (SE 489.8), 882.6 (SE 515.7), 977.3 (SE 515.1), 953.1 (SE 515.2), and 93.6 (SE 550.6), respectively. Felling gaps (-0.365; 95% CI, -0.74 to -0.03) and primary skid trails (-0.627; 95% CI, -0.99 to -0.27) had small negative effects on overall palm regeneration whereas log landings had a large negative effect (-2.93; 95% CI -3.30 to -2.47), where overall palm regeneration was scarce (Figs. 2 and 3). Secondary skid trails had a non-significant effect on overall palm regeneration (-0.20; 95% CI -0.54 to 0.13) with NADA sites having the most unexplained variation (1.59; 95% CI, -0.21 to 3.94). This pattern of sparse regen

eration on log landing was also observed for all woody plants <1 m (Fig. 4).

The NMDS indicated clustering of log-landing plots (Fig. 5), but that pattern seems more related to overall regeneration scarcity than to any systematic effects on palm species composition. *Guassia* was more associated with NADA sites while *Cryosophila* was well represented across all disturbance categories (Fig. 3).

# 4. Discussion

The ground area affected by logging in our study using RIL practices (7.0%) was about half that reported in a similar study in a nearby forest in Belize (12.9%) that was harvested at a fifth the intensity (2.7 vs. 0.5 trees ha<sup>-1</sup>, respectively) but without the benefits of RIL practices (Whitman et al., 1997). The observed reduction in disturbance can be attributed mostly to a five-fold reduction in skid trail length per tree harvested in the non-RIL  $(209.6 \text{ m tree}^{-1} \text{ harvested})$  and our RIL study  $(39.4 \text{ m tree}^{-1} \text{ har-})$ vested). RIL skid trails were also 5% narrower than in the earlier non-RIL harvested forest (3.4 m vs. 3.6 m, respectively). Other studies confirm the benefits of skid trail and road planning (e.g., Gullison and Hardner, 1993; Griscom et al., 2014), with variation of observed logging impacts also directly associated with harvest intensity even where RIL guidelines are followed (Burivalova et al., 2014). For example, in a structurally similar forest in Bolivia where 4.7 trees  $(12.1 \text{ m}^3 \text{ ha}^{-1})$  were harvested, as compared to 2.7 trees  $(2.9 \text{ m}^3 \text{ ha}^{-1})$  at our study site, the overall damage approached 50%, seven-times what we observed in Belize (Jackson et al., 2002). A large proportion of this difference is due to the sizes of trees harvested in Bolivia, which averaged 81 cm DBH compared to 55 cm DBH in Belize, and that resulted in much larger felling gaps in the former (591 m<sup>2</sup> vs. 90 m<sup>2</sup>), but roads in



**Fig. 2.** Regression coefficients for palm seedling abundance based on logging disturbance categories from a generalized linear mixed-effect model with palm species as random effects. Bars indicate the 95% credible intervals (CI) based on the posterior draw, and points indicate the mean effect size. Coefficients with 95% CIs that do not cross the zero line are statistically significant. The magnitude of coefficients can be interpreted as the effect size of each disturbance category on overall palm recruitment across species. N = 11 plots of 40 m<sup>2</sup> in each habitat type. NADA = not directly affected area; GAP = felling gaps; SS = secondary skid trails; PS = primary skid trails; and, LL = log landings.



Fig. 3. Model predictions for species-specific baseline palm regeneration abundance across logging disturbance categories (abbreviations as in Fig. 2). Seedling densities are presented for 40 m<sup>2</sup> plots.

Bolivia were also 4 m wider than at our study site in Belize (11 m vs. 7 m).

Logging impacts on palm seedling densities and species composition in our study site were mostly restricted to the log landings that covered only 0.4% of the logged area. The small impacts of skid trails and felling gaps on palm regeneration seem attributable to limited soil scarification and compaction. Insofar as recruitment depends on the nearby presence of parent trees (Darrigo et al., 2016) and skidder drivers, in our experience, avoid large trees but not palms, we expected a larger impact of skid trails on palm recruitment. What we observed, in contrast, was that in the course of knocking down and running over fruit-bearing palm trees, the skidders pushed viable palm seeds into the soil in areas where they experienced excellent conditions for germination and survival (e.g., the log landing outlier in Fig. 4). Overall, the canopy openings and soil disturbances caused by tree felling and skid trail opening created suitable sites for palm seedling establishment and growth. In contrast, on log landings where most of the surface soil was removed and most plants were uprooted, light-demanding pioneer trees, shrubs, and herbs with well-dispersed seeds were favoured.



Fig. 4. Relative abundance (percentage) of palms in relation to all woody seedlings <1 m tall (both palms and other woody regeneration) along a gradient of increasing disturbance (abbreviations as in Fig. 2). Boxplots depict the median and inter-quartile ranges.



**Fig. 5.** Ecological distance (Bray–Curtis) between all pairs of sites based on palm species abundances. Values are presented in a 2-dimensional ordination space using nonmetric multidimensional scaling (NMDS). Sites located closer to species in the ordination space are more likely to have those species well represented (abbreviations as in Fig. 2).

We also expect that palms seldom successfully recruited onto log landings because they suffered from drought and heat damage in the large openings.

The loss of reproductive individuals due to skid trail construction and use may result in reduced seed rain in future years, a consequence that should be monitored. Nevertheless, we expect that given the nearly 10% increase in light intensities near the ground on skid trails relative to areas not directly affected by logging, as well as otherwise suitable growing conditions (Darrigo et al., 2016), the long-term legacy of skid trails will be linear arrays of palms. In many tropical forests, palms are good indicators of historical human occupancy (Bush et al., 2015) and contemporary responses similar to those we predict for the skid trails are reported for babassu palm (*Attalea speciosa*) dominated groves in Amazonian cattle pastures (Anderson et al., 1991). In regards to the lack of *Attalea* in our study area, we expect that this finding is due to our not sampling near archaeological sites where this very useful species is often clustered.

Our findings indicate that RIL carried out at the observed tree harvest intensity (2.7 trees ha<sup>-1</sup>) did not affect palm seedling regeneration except on log landings where overall plant densities were still low 1-year after selective logging. Given that the log landings are to be used again in 40 years when the forest is next slated for logging, regeneration scarcity is perhaps not of great concern. Although we cannot assume that the observed pattern will be maintained over time, our findings nevertheless suggest compatibility between low-intensity RIL harvests and conservation of palms, a keystone plant group in tropical forests. RIL at lowintensity for timber production at scales of 10 ha to 100,000 ha may represent an opportunity for conservation of important plant groups within production landscapes, which is generally framed as land-sharing (e.g., Fischer et al., 2014; Phalan et al., 2011). Given the growing pressure for forest conversion to industrial export agriculture and the high likelihood of devastating hurricanes, efforts to increase the profitability and sustainability of timber stand management seem warranted to maintain forest structure and associated biodiversity.

## Acknowledgements

Financial support was provided by the Energy and Climate Partnership of the Americas (http://ecpamericas.org/), with additional support from the Yalbac Ranch and Cattle Corporation. We wish to thank J. Roberson of Yalbac Ranch and J. Alavalapati from Virginia Tech University for facilitating this workshop, Gallon Jug Estate for providing lodging and support, and R. Goodman for useful comments.

#### References

- Abrahamson, W.G., 1999. Episodic reproduction in two fire-prone palms, Serenoa repens and Sabal etonia (Palmae). Ecology 80, 100–115. http://dx.doi.org/ 10.2307/176982.
- Anderson, A., May, P.H., Balick, M., 1991. The Subsidy From Nature: Palm Forests, Peasantry, and Development on an Amazon Frontier. Columbia University Press, New York. http://dx.doi.org/10.1016/0169-5347(92)90157-7.
- Balick, M.J., Beck, H.T., 1990. Useful Palms of the World. A Synoptic Bibliography. Columbia University Press, New York.
- Berry, N.N.J., Phillips, O.L., Lewis, S.S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M., Ong, R.C., Hamer, K.C., 2010. The high value of logged tropical forests: Lessons from northern Borneo. Biodivers. Conserv. 19, 985–997. http://dx.doi.org/10.1007/s10531-010-9779-z.
- Bicknell, J.E., Struebig, M.J., Edwards, D.P., Davies, Z.G., 2014. Improved timber harvest techniques maintain biodiversity in tropical forests. Curr. Biol. 24, R1119–R1120. http://dx.doi.org/10.1016/j.cub.2014.10.067.
- Burivalova, Z., Şekercioğlu, Ç.H., Koh, L.P., 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. Curr. Biol. http://dx.doi.org/10.1016/j. cub.2014.06.065.
- Bush, M.B., McMichael, C.H., Piperno, D.R., Silman, M.R., Barlow, J., Peres, C.A., Power, M., Palace, M.W., 2015. Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. J. Biogeogr. http://dx.doi.org/10.1111/ jbi.12638, n/a-n/a.
- Cannon, C., Peart, D., Leighton, M., 1998. Tree species diversity in commercially logged bornean rainforest. Science 281, 1366–1368.
- Cherrington, E.A, Ek, E., Cho, P., Howell, B.F., Hernandez, B.E., Anderson, E.R., Flores, A.I., Garcia, B.C., Sempris, E., Irwin, D.E., 2010. Forest Cover and Deforestation in Belize: 1980–2010. Serv. Tech. Rep. 1980–2010.
- Cherrington, E.A., Cho, P., Ivanna, W., Santos, T.Y., Escalante, A., Nabet, J., Usher, L., 2012. Executive Summary: Forest Cover and deforestation in Belize, 2010–2012. Panama City.
- Darrigo, M.R., Venticinque, E.M., dos Santos, F.A.M., 2016. Effects of reduced impact logging on the forest regeneration in the central Amazonia. For. Ecol. Manage. 360, 52–59. http://dx.doi.org/10.1016/j.foreco.2015.10.012.
- de Avila, A.L., Ruschel, A.R., de Carvalho, J.O.P., Mazzei, L., Silva, J.N.M., Lopes, J. do C., Araujo, M.M., Dormann, C.F., Bauhus, J., 2015. Medium-term dynamics of tree

species composition in response to silvicultural intervention intensities in a tropical rain forest. Biol. Conserv. 191, 577–586. http://dx.doi.org/10.1016/j. biocon.2015.08.004.

- Duah-Gyamfi, A., Swaine, E.K., Adam, K.A., Pinard, M.A., Swaine, M.D., 2014. Can harvesting for timber in tropical forest enhance timber tree regeneration? For. Ecol. Manage. 314, 26–37. http://dx.doi.org/10.1016/j.foreco.2013.11.025.
- Emilio, T., Quesada, C.A., Costa, F.R.C., Magnusson, W.E., Schietti, J., Feldpausch, T.R., 2014. Soil physical conditions limit palm and tree basal area in Amazonian forests. Plant Ecol. Divers. 7, 1–15.
- Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land sparing versus land sharing: moving forward. Conserv. Lett. 7, 149–157. http://dx.doi.org/ 10.1111/conl.12084.
- Gabry, J., Goodrich, B., 2016. rstanarm: Bayesian Applied Regression Modeling via Stan, R package version 2.9.0-1.
- Goodman, R.C., Phillips, O.L., Del Castillo Torres, D., Freitas, L., Cortese, S.T., Monteagudo, A., Baker, T.R., 2013. Amazon palm biomass and allometry. For. Ecol. Manage. 310, 994–1004. http://dx.doi.org/10.1016/j.foreco.2013.09.045.
- Griscom, B., Ellis, P., Putz, F.E., 2014. Carbon emissions performance of commercial logging in East Kalimantan, Indonesia. Glob. Chang. Biol. 20, 923–937. http://dx. doi.org/10.1111/gcb.12386.
- Gullison, R.E., Hardner, J.J., 1993. The effects of road design and harvest intensity on forest damage caused by selective logging: empirical results and a simulation model from the Bosque Chimanes. Bolivia. For. Ecol. Manage. 59, 1–14. http:// dx.doi.org/10.1016/0378-1127(93)90067-W.
- Henderson, A., Tomlinson, P.B., 1991. The structural biology of palms. Brittonia 43, 65. http://dx.doi.org/10.2307/2807180.
- Jackson, S.M., Fredericksen, T.S., Malcolm, J.R., 2002. Area disturbed and residual stand damage following logging in a Bolivian tropical forest. For. Ecol. Manage. 166, 271–283. http://dx.doi.org/10.1016/S0378-1127(01)00681-8.
- Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K.A., Massachusetts, I.O.T., Holland, G. J., Landsea, C.W., Held, I.M., Kossin, J.P., Srivastava, A.K., Sugi, M., 2010. Tropical cyclones and climate change. Nat. Geosci. 3, 157–163. http://dx.doi.org/ 10.1038/ngeo779.
- Lemmon, P., 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2, 314–320.
- McCloskey, T.A., Keller, G., 2009. 5000 year sedimentary record of hurricane strikes on the central coast of Belize. Quat. Int. 195, 53–68. http://dx.doi.org/10.1016/j. quaint.2008.03.003.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.M., Wagner, H., 2010. Community ecology package: vegan (Ordination, Diversity and Dissimilarities). In: R: A Language and Environment for Statistical Computing. p. http://vegan.r-forge.rproject.org/.
- Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333, 1289–1291.
- Putz, F.E., Sist, P., Fredericksen, T., Dykstra, D., 2008. Reduced-impact logging: challenges and opportunities. For. Ecol. Manage. 256, 1427–1433. http://dx.doi. org/10.1016/j.foreco.2008.03.036.
- R CORE TEAM, 2010. R: A Language and Environment for Statistical Computing.
- Schwartz, G., Lopes, J.C., Kanashiro, M., Mohren, G.M., Peña-Claros, M., 2014. Disturbance level determines the regeneration of commercial tree species in the eastern Amazon. Biotropica 46, 148–156.
- ter Steege, H. et al., 2013. Hyperdominance in the Amazonian tree flora. Science 342, 1243092.
- Whitman, A.A., Brokaw, N.V.L., Hagan, J.M., 1997. Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. For. Ecol. Manage. 92, 87–96. http://dx.doi.org/10.1016/S0378-1127(96)03941-2.