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1 Tropical forest light regimes in a human-modified landscape

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22

23 **Abstract**

24 Light is the key energy input for all vegetated systems. Forest light regimes are complex, with
25 the vertical pattern of light within canopies influenced by forest structure. Human disturbances in
26 tropical forests impact forest structure, and hence may influence the light environment and thus
27 competitiveness of different trees. In this study we measured vertical diffuse light profiles along
28 a gradient of anthropogenic disturbance, sampling intact, logged, secondary and fragmented sites
29 in the biodiversity hotspot of the Atlantic forest, south-east Brazil, using photosynthetically
30 active radiation (PAR) sensors and a novel approach with estimations of vertical light profiles
31 from hemispherical photographs. Our results show clear differences in vertical light profiles with
32 disturbance – fragmented forests are characterized by rapid light extinction within their low
33 canopies, while the profiles in logged forests show high heterogeneity and high light in the mid
34 canopy despite decades of recovery. The secondary forest showed similar light profiles to intact
35 forest, but with a lower canopy height. We also show that in some cases the upper canopy layer
36 and heavy liana infestations can severely limit light penetration. Light extinction with height
37 above the ground and depth below the canopy top was highest in fragmented forest and
38 negatively correlated with canopy height. The novel, inexpensive, and rapid methods described
39 here can be applied to other sites to quantify rarely measured vertical light profiles.

40 **Key Words:** Atlantic forest; Brazil; canopy; degraded; disturbance; extinction coefficient;
41 fragment; montane; radiation; secondary; structure; vertical profile.

42

43 **Introduction**

44 Light is a key environmental variable driving plant productivity by providing energy for
45 photosynthesis. Photosynthetic rates respond to changes in incoming radiation, and plants also

46 show acclimation to the prevailing growth irradiance, with lower rates of photosynthesis and
47 respiration and altered leaf structure under shaded conditions (Chen et al. 2014). In tropical
48 forests, which constitute a globally significant store of carbon (Pan et al. 2011) and biodiversity
49 (Dirzo and Raven 2003), the light environment is highly complex (Chazdon and Fetcher 1984)
50 and tree species life histories are often associated with light availability (e.g. Poorter et al. 2006).
51 Diurnal and seasonal patterns of incoming radiation can be easily understood based on solar
52 geometry and the movements of clouds. However, the attenuation of light within the forest
53 canopy is determined by the vertical structure of stems, leaves, and their optical properties
54 (Binkley et al. 2013). Hence, forest structure is a driver of light availability within canopies,
55 which can then impact the physiological rates of trees.

56

57 Anthropogenic disturbances, such as selective logging, clear felling, fragmentation, and fire,
58 affect forest structure. For example, secondary, logged, fragmented forests, and forest edges
59 typically contain fewer large trees than intact forest (e.g. Laurance et al. 1997, Paula et al. 2011,
60 Berenguer et al. 2014). The structure of trees themselves may also be different in disturbed
61 forests due to changes in species composition with the proliferation of pioneers (Michalski et al.
62 2007, Paula et al. 2011, Laurance et al. 2011). Early successional species have different
63 architectures to shade tolerant species with narrower crowns and taller heights (Poorter et al.
64 2006, Montgomery and Chazdon, 2001), and tree architecture has been shown to change after
65 selective logging with lower tree heights for a given diameter (Rutishauser et al. 2016). Hence,
66 light regimes in human-modified forests may differ from those in intact forests due to differences
67 in tree size-class distributions, species composition, and allometry.

68

69 The majority of research conducted thus far into light environments in human-modified forests
70 focuses on the understory due the logistical challenges of working in the canopy. Even with
71 differing structures, the percentage of light reaching the forest floor (transmittance) is typically
72 low (1-2 %) and may vary little between intact, secondary and selectively logged forest (Nicotra
73 et al. 1999, Montgomery and Chazdon 2001). However, others have shown higher understory
74 light levels in selectively logged forests (Yamada et al. 2014, Osazura-Peters et al. 2015) and
75 decreasing light with secondary forest age (Denslow and Guzman 2000, Lebrija-Trejos et al.
76 2011). Spatial heterogeneity in understory light transmittance between gap and closed areas
77 within intact forest has been quantified (e.g. Chazdon and Fetcher 1984, Canham et al. 1990,
78 Rich et al. 1993), and shows less variation in secondary forests (Nicotra et al. 1999). Fragment
79 edges are known to have brighter, hotter microclimates compared with forest interiors (Newmark
80 2001, Ewers and Banks-Leite 2013, Magnago et al. 2015), although time and structure
81 development since fragmentation, and land-use adjacent to the fragment affect the strength of the
82 difference (Didham and Lawton 1999).

83

84 Much less information is available on the vertical profile of light, especially in human-modified
85 forests. The vertical pattern of light transmission is important for our understanding of forest
86 productivity, growth and dynamics (as inferred from LiDAR data, Stark et al. 2012, Stark et al.
87 2015). A small number of datasets have been collected for intact tropical forests with direct
88 measurements of light profiles (Yoda 1974, Torquebiau 1988, Maass et al. 1995, Anhuf and
89 Rollenbeck 2001, Wirth et al. 2001, Parker et al. 2005) or of leaf area profiles Clark et al. 2008).
90 However, most studies are limited to very small sample numbers (but see Parker et al. 2005,
91 Clark et al. 2008), or to a small footprint from crane-based studies (Anhuf and Rollenbeck 2001,

92 Kitajima et al. 2005). Data on 3D forest structure (Lefsky et al. 2002) and associated light
93 environments (Parker et al. 2001, Stark et al. 2012) can be estimated from LiDAR (light
94 detection and ranging), which increases the spatial coverage of measurements. However, LiDAR
95 technology remains expensive and produces vast datasets that can be challenging to analyse.
96 Diffuse light conditions (as opposed to direct light conditions) are convenient for the direct
97 measurement of vertical light profiles because it avoids the high variability in light conditions
98 due to sun-flecks (e.g. Parker et al. 2002 found profiles measured under an overcast sky where
99 smoother than those under clear sky) and the profiles produced reflect the under-lying forest
100 structure. Further, diffuse light can penetrate deeper into forest canopies than direct light
101 resulting in more efficient canopy light use under diffuse light (Alton et al. 2007). Therefore,
102 here we focus on diffuse light.

103

104 With this paper, we tackle the data-gap concerning vertical light profiles for intact and human-
105 modified Atlantic forests. This work will add to previous knowledge of understory light patterns
106 in intact and human-modified forests and provide valuable new data for a threatened biodiversity
107 hotspot which has experienced substantial deforestation (Ribeiro et al. 2009). As datasets on
108 vertical light profiles are rare, especially in disturbed forests, the results will be of use to test
109 light interception schemes for forest models. We use two methods to measure light profiles –
110 directly with photosynthetically active radiation (PAR) sensors, and indirectly with vertical
111 profiles of hemispherical photographs. Both methods are low-cost and repeatable across
112 landscapes. The aim of the paper is to characterize the vertical light environments of forests
113 along a disturbance gradient of intact, selectively logged, secondary, and fragmented forest,
114 accounting for spatial variation within sites. We expect that along the gradient from least to most

115 disturbed forests (intact < logged < secondary < fragment) light will penetrate further into the
116 canopy due lower canopy closure and smaller tree crowns with increasing severity of
117 disturbance.

118

119 Materials and Methods

120 *Study sites*

121 The study was carried out in and around Núcleo Santa Virginia of the Serra do Mar State Park in
122 the municipality of São Luis do Paraitinga, São Paulo state, Brazil. The park is home to the
123 largest contiguous patch of Atlantic forest remaining, running along a steep coastal mountain
124 range. The forest is classified as montane moist dense forest (Veloso et al. 1991, Oliveira-Filho
125 and Fontes 2000) and contains palms, tree ferns, bamboos, epiphytes and lianas in addition to
126 dicot trees. Mean annual precipitation is 2300 mm with a dry season in July and August, mean
127 annual temperature is 17°C (Joly et al. 2012) and fog occurs frequently (Rosado et al. 2010).
128 Inland from the park the landscape is pastoral with patches of privately owned forest within a
129 matrix of cattle pasture and occasional eucalyptus plantations. Terrain both inside and outside the
130 park is hilly. Climate of the inland fragmented area is drier and hotter than the continuous forest,
131 with the presence of some deciduous tree species and no tree ferns.

132

133 The sampling took advantage of a network of 1-ha permanent forest inventory plots within the
134 Serra do Mar State Park (established under the Biota Functional Gradients project, Joly et al.
135 2012) and newly established plots within fragments outside the reserve (Table 1). Data was
136 collected from four plots within the continuous forest of the park, two in an area of intact forest
137 (plots K and M in Joly et al. 2012), one in an area that had been selectively logged before the

138 establishment of the park in 1977 (plot N in Joly et al. 2012), and one in a regenerating area clear
139 cut for charcoal production before park establishment that is considered a mid-stage secondary
140 forest (Marchiori et al. 2016). These plots are referred to as intact-K, intact-M, logged and
141 secondary in the text. Two forest fragments were also sampled, one near the community of
142 Catuçaba (fragment-C) and one near the town of Lagoinha (fragment-L). In fragments, two plots
143 of 10 x 250 m were established, one at the edge (approx. 30 m from edge) and one in the interior
144 (approx. 100 m from edge). Both fragments are adjacent to cattle pasture. Whilst the precise
145 history of the fragments is unknown, historical aerial imagery show that fragment-C has been
146 forested since before 1962, whilst in fragment-L the edge plot was pasture and the interior plot
147 forested in 1962. All trees > 4.8 cm diameter at breast height (dbh) were inventoried with
148 diameter, species identification and co-ordinates in the plot recorded.

149

150 *Light profile measurements*

151 19 PAR sensors were built following the method of Fielder and Comeau (2000). For each sensor
152 a gallium arsenide phosphorus (GaAsP) photodiode (G1118, Hamamatsu, Japan) was housed in
153 acrylic and aluminium with a cos-sine correcting diffuser. Each sensor was individually
154 calibrated against a LI-COR 190 quantum sensor (LI-COR Inc., Nebraska, USA). One sensor
155 connected to a CR200 datalogger (Campbell Scientific, Utah, USA) was used as an open sky
156 reference located either in a clearing or atop a canopy tower located in the secondary plot. All
157 other sensors were connected to an AM16/32 multiplexer and CR800 datalogger (Campbell
158 Scientific, Utah, USA) to take simultaneous measurements from each sensor. Differential voltage
159 measurements were used for the profile sensors and single ended measurements for the open sky
160 sensor. To measure a profile a thin rope was installed over a high tree branch using a Big Shot

161 catapult (Sherrill Tree, North Carolina, USA) from which the sensors were suspended. Each
162 sensor was positioned on a support structure consisting of a plastic bar bolted to a plastic ring,
163 with each support connected to the next at 1 m intervals with Kevlar tape (Fig. 1). Data were
164 collected every 30 seconds and the average was recorded each minute.

165

166 Fieldwork was carried out between March and October 2016. Within each plot, 10 – 12 locations
167 were sampled. Each sampling point was at least 20 m away from other sampling points to ensure
168 the independence of the light environments. For each sampling point, a 20 x 20 m subplot (10 x
169 10 m for fragments) was preselected under a stratified design to evenly cover each plot. Within
170 the chosen subplot, the tallest suitable tree for measurements was selected. Trees considered
171 suitable possessed a strong branch with a clear line of sight from the ground to enable rope and
172 sensor installation. For one sample (point 2 in the secondary plot) the sensors were suspended
173 from a narrow canopy tower. The profile sensor was 18 m long, so for branches higher than 18 m
174 the sensors were pulled to the highest possible position and the bottom portion of the profile
175 (maximum 6 m) were not measured. Each point was sampled for a minimum of one hour and
176 maximum of 3 days, always including a period of diffuse light conditions (either an overcast sky
177 or dawn/dusk). The height of the highest leaves of the sampled tree was measured either with a
178 laser rangefinder (Forestry Pro, Nikon, Japan), hypsometer (Vertex IV, Haglof, Sweden) or
179 visual estimation.

180

181 To produce the light profile for each point, the data was manually examined to locate time
182 periods of measurements under diffuse conditions (in order to avoid the influence of sunflecks
183 and sun angle on the light profiles). The mean PAR recorded by each sensor as a percentage of

184 the open sky reference PAR (% transmission) was calculated across all data points collected
185 under diffuse conditions.

186

187 Measuring light profiles during different times of day and months of the year could lead to
188 inaccurate determination of vertical profiles if varying sun angle influences the profile even
189 under diffuse conditions. Strongly seasonal leaf phenology could also result in seasonal variation
190 in the light profile. We collected light profile data continuously from November 2015 – July
191 2016 from a narrow canopy tower in the secondary forest plot. This showed that the light profiles
192 determined at dusk and at dawn were very similar (Appendix S1: Fig. S1), hence change in sun
193 angle during the day does not affect the profile. Comparing profiles produced for different
194 months showed that the shape of the profile was consistent over the year, but that the extent of
195 light transmission varied over the year (Appendix S1: Fig. S2), likely due to seasonality of leaf
196 phenology. Light transmission was lowest, and therefore leaf area highest, in April, coincident
197 with austral autumn and the transition to the drier, cooler season. The reduction in transmission
198 between months of highest and lowest value (November - April) was low (mean 7.2 % across all
199 heights), but quite variable (sd 7.6 %) with higher reductions in the upper canopy (above 13 m)
200 than lower down. Hence, the general shape of the profile does not vary over the year, but the
201 absolute values of % transmission may slightly alter.

202

203 To calculate a mean light profile for each plot, the % transmission at each 1 m height above the
204 ground was averaged across each sampling point. For fragments, data from the edge and interior
205 transects were combined. For heights above the top of the sampled tree % transmission was
206 assumed to be 100 %. As the highest sensor was necessarily below a branch, there was an

207 unsampled section of the light profile between the top sensor and the top of the tree. The %
208 transmission for these unsampled sections was estimated using a linear interpolation from 100 %
209 transmission at the top of the tree to the % transmission measured at the height of the top sensor.
210 For profiles where the bottom sensor was above 1 m, transmission values for all heights below
211 the bottom sensor were assumed to be equal to that at the bottom sensor. In the figures measured
212 data points and interpolated or extrapolated data points are differentiated with different symbols.
213

214 In addition to the mean profile based on height above the ground, a mean profile using depth
215 from the canopy top (d) was also produced. This means that all data points collected at the top of
216 each sampled tree are at the same depth (0 m), rather than at different heights above the ground.
217 We included depths up to the mean sample tree height for each plot (i.e. all data points from the
218 canopy top downwards over a vertical distance equal to the plot mean sample tree height). Where
219 the sample tree was shorter than the plot mean sample tree height % transmission was
220 extrapolated downwards.

221

222 *Quantitative comparison of light profiles between sites*

223 To quantify differences in the mean light profiles between sites, we estimated the extinction
224 coefficient (k_z) with height above the ground (z) for each mean plot profile using equation 1

225

$$226 \quad \% \text{ Transmission } (z) = a + \exp(k_z z) \quad \text{equation 1}$$

227

228 The parameter a is the % transmission at ground level. As not all upper sections of the plot mean
229 profile fit the exponential decay function (section *Variation in light profiles with disturbance*
230 *history*), we excluded such sections from the analysis.

231

232 In order to include all the upper profile in an estimation of the extinction coefficient, we also
233 estimate the extinction coefficient with depth (d) from the top of the canopy (k_d). using equation
234 2. Note also the negative use of the extinction coefficient in comparison to equation 1.

235

236 % *Transmission* (d) = $a + (100 - a) \cdot \exp(-k_d d)$ equation 2

237

238 Parameters (a, k_z, k_d) were estimated using non-linear least squares with the function ‘nls’ in the
239 statistical program R 2.15.1 (R Core Team 2012).

240

241 *Light profiles from hemispherical photos*

242 In addition to the data collected using PAR sensors, for 45 profiles we also collected a vertical
243 profile of hemispherical photos. Photographs were taken with a digital SLR camera (D3100,
244 Nikon Corporation, Japan) and 4.5mm circular fisheye lens (F2.8 EX DC, Sigma, USA) using
245 mode P and exposure compensation of -1 EV. One of the PAR sensor support structures was
246 adapted to serve as a cradle for the camera which was then attached to the rope; a gimbal was
247 considered unnecessary since hand-leveling has proven reliable for plant area index estimates
248 from hemispherical photos (Origo et al. 2017). The camera was programmed to take one photo
249 every 2 minutes, and was pulled higher into the canopy (at *c.* 2 m intervals in the continuous
250 forest and 1 m intervals in the fragments) between each photo. The 2 minute interval was

251 typically long enough for the camera to stop rotating on the rope which was a common
252 occurrence. The photographs were then used to estimate % transmission. The images were
253 thresholded (converted to black for vegetation and white for sky) using only the blue channel
254 following Pfeifer et al. (2012) using the Ridler and Calvard (1978) thresholding algorithm. The
255 thresholded images were then analysed in the program Hemisfer (WSL, Switzerland) to
256 determine % transmission (Schleppi et al. 2007, Thimonier et al. 2010). All five annuli of the
257 image were used, corresponding to 180° field of view. The apparatus support strings were visible
258 in the image and were classified as vegetation. A separate analysis of 8 manipulated images of
259 strings only showed that they covered 8 % of the image. As it is likely that at least some of the
260 support strings covered vegetation area in the image, we did not attempt to correct for them. As
261 such, the % transmission estimations from the images may underestimate up to 8 %, but only in
262 cases where the transmission is very high.

263

264 All data analyses were carried out in R 2.15.1 (R Core Team 2012).

265

266 Results and Discussion

267 *The shapes of light profiles*

268 The light profiles for each sample point are presented in Appendix S1: Fig. S3 and examples
269 from each plot in Fig. 2. We believe this is the first study to present spatially replicated vertical
270 light profiles along a degradation gradient. The most obvious pattern in Appendix S1: Fig. S3 is
271 the decrease in sample tree height along the disturbance gradient, being tallest in the intact plots
272 and shortest in the fragments (Table 2). The low canopy heights in the fragments are likely a
273 reflection of the high level of degradation in these small fragmented forests. Other studies have

274 shown that short-statured, pioneer and early successional species typically dominate Atlantic
275 forest fragments (e.g. Tabarelli et al. 1999, Oliveira et al. 2008, Paula et al. 2011) as a result of
276 altered seed dispersal (Costa et al. 2012) and a hotter, drier microclimate (Kapos 1989) causing
277 biotic homogenization and a shift towards composition typical of secondary forests (Joly et al.
278 2014).

279

280 A second point of interest is the variation in the shapes of the light profiles (Fig. 2, Appendix S1:
281 Fig. S3). Considering all profiles, we can qualitatively split the samples into three categories:
282 profiles that are dark throughout (e.g. Fig. 2a,e), profiles that decline from high to low light (e.g.
283 Fig. 2b,f,k), and profiles that show inversions, or points where the available light is greater than
284 at heights above (e.g. Fig. 2c,h,j). All three categories occur in all plots, except for dark profiles
285 in the logged plot. The dark profiles can be considered, to a certain extent, a consequence of our
286 sampling methodology that necessarily requires the top measurement to be below a branch. As it
287 was not possible to sample through the top of the crown to the canopy top we miss the initial
288 light attenuation, though we can still estimate this using our data. As we use a linear interpolation
289 between the top of the tree and the top sensor, we could slightly overestimate % transmission in
290 the estimations at these heights, as the decline is unlikely to be completely linear, and we are
291 assuming that there will be 100 % transmission at the top of the sample tree, whereas in reality
292 there is likely already some shading from neighbouring crowns of tall trees. As these interpolated
293 points are a minority compared with the measured points (on average 2.3 m of each profile is
294 interpolated), this likely does not strongly influence our results. Dark profiles in the fragments
295 were typically found in subplots with a dense liana layer covering the tree crowns. Lianas are
296 known to be particularly abundant in disturbed areas (Schnitzer and Bongers 2011), and high

297 abundances of small lianas have been found in other studies of forest fragments (Oliveira-Filho
298 et al. 1997, Laurance et al. 2001, Farah et al. 2014). This high liana abundance can have a strong
299 impact on the light environment, restricting the penetration of light even very close to the canopy
300 top, supporting other work that showing that lianas can reduce forest productivity (van der
301 Heijden et al. 2015, Lai et al. 2017). Whilst lianas, or high epiphyte loads which are common in
302 the continuous forest, may also be a cause of the dark profiles in the continuous plots, our
303 inability to reach the canopy top was more prevalent in the continuous forest than in the
304 fragments, and the influence of the interpolations is likely higher. Despite this limitation, the
305 dark profiles are still of interest as they show that in some cases the % transmission is already
306 very low just below the canopy top; light transmission can be less than 5 % as high up as 18 m,
307 or 5 m below the top of the crown (Fig. 2a). This is due to the dense upper canopy absorbing
308 substantial light – up to 95 % in this study.

309

310 The profiles with inversions were somewhat unexpected as they do not conform to the broadly-
311 assumed exponentially decaying light availability profile. Some of the inverted profiles may be a
312 result of the methodology with direct shading of the top sensor by the branch from which the
313 sensors were suspended (e.g. Fig. 2h). However, in others the inversion occurs further down (e.g.
314 Fig. 2c). Whilst there is little data available on light profiles with spatially extensive sampling
315 from other sites, inversions in the light profile have been observed in intact tropical forest in
316 Venezuela (Anhuf and Rollenbeck 2001) and in temperate coniferous (Parker 1997) and
317 deciduous (Parker et al. 1996) forests. These inversions are due to incoming light through lateral
318 canopy gaps. In this study, the inversions are a particularly common occurrence in the logged
319 plot; selective logging removes large crowns creating gaps in the upper canopy.

320

321 *Variation in light profiles with disturbance history*

322 A feature of the mean height - % Transmission profile produced for each plot (Fig. 3) is the
323 initial small declines in available light before rapid light attenuation occurs. This is due to the
324 averaging across individual profiles with different canopy heights, and the extent of this effect
325 reflects spatial heterogeneity in tree height. In contrast, the mean depth - % Transmission profiles
326 are not affected by heterogeneity in tree height and show exponential decline in light from
327 canopy top downwards. In plots where there are few tall sample trees and many shorter ones
328 (e.g. logged and fragment-L) this slow attenuation in height-based profiles continues further
329 down the canopy. Interestingly, fragment-C also shows this slow decline, but without the
330 characteristic pattern of few large trees to explain it. The distribution of sample tree size is quite
331 different between fragment-C and fragment-L, yet fragment-C does not have higher attenuation
332 in its upper canopy. This may be due to an effect of season of sampling as, whilst in the
333 continuous plots all species are evergreen, deciduous species are present in the fragments and
334 some had lost their leaves at the time of sampling fragment-C (end of the dry season). Leaf
335 shedding alters the patterns of light below tree crowns (Gandolfi et al. 2007) and hence likely
336 influenced our measurements in fragment-C. In fragment-L, there is strong light attenuation
337 between 6 to 8 m height, just below the median sample tree height. In this plot, especially in the
338 edge transect, trees were similarly sized with a homogenous canopy layer around 8 m high,
339 resulting in strong light absorption at this height.

340

341 The mean profiles of both height and depth show that the inversions seen in the individual
342 profiles are maintained in mean profile for the logged plot (Fig. 3c). While inversions are to be

343 expected in any forests with a heterogeneous canopy, the pattern should not be visible in the
344 mean profile given sufficient sampling otherwise it would suggest a source of light within the
345 forest (Parker 1997). The fact that this has occurred in the logged forest only suggests that the
346 canopy in this plot is more heterogenous than all other forest types studied. This prevalence of
347 inverted profiles in the logged plots is despite the fact that the logging occurred over 40 years
348 ago. One might expect that gaps produced by logging (or natural tree death) would be filled in
349 over this timescale by the remaining trees growing laterally (Young and Hubbell 1991) or new
350 trees filling the space, thereby removing these light gaps. However, recovery of forest structure
351 (biomass and/or basal area) in selectively logged forests takes considerable time, with
352 estimations in the order of decades, ranging from 10 – *c.* 100 years depending on the logging
353 intensity (Blanc et al. 2009, Huang and Asner 2010, Bonnelli et al. 2011, West et al. 2014,
354 Rutishauser et al. 2015). In this case, the biomass of the logged plot (274 Mg ha⁻¹, Vieira et al.
355 2011) is similar to three intact plots (including the two in this study) at the site (242-323 Mg ha⁻¹,
356 Vieira et al. 2011) suggesting that the biomass at least has recovered in this plot (though the pre-
357 logging biomass of the plot is unknown). Rutishauser et al. (2016) show that the diameter –
358 height allometry of trees of remnant trees in logged forest varies from intact forest, with shorter
359 trees for a given diameter in logged forest, an effect that was present even 25 years after the
360 disturbance. They suggest that the height reduction is a consequence of crown development at
361 lower heights due to the altered light environment. This reduction in height growth could
362 maintain canopy heterogeneity rather than filling in gaps.

363

364 Both of the intact plots show a similar pattern, with a sharp initial decline in light through the
365 upper canopy and a slower decline below (Fig. 3a,b). The profile shapes of the intact plots are

366 similar to those directly measured from other sites in Venezuela (Anhuf and Rollenbeck 2001)
367 and estimated from LiDAR in the central Amazon (Stark et al. 2012).

368

369 Interestingly, within the continuous forest, the shape of the secondary forest profile is more
370 similar to the intact forest than the logged forest (Fig. 3a-d). Below 10 m height, there is very
371 little difference between the secondary and intact profiles whilst there is considerably more light
372 transmission in the logged plot, with significantly higher % Transmission at 10 m height in
373 logged plot 37.6 ± 23.1 % (mean \pm sd) than in the secondary, intact-K and intact-M plots with
374 13.3 ± 9.9 , 14.8 ± 12.3 , 13.3 ± 9.1 respectively (Anova, $F = 7.1$, $df = 3$, $p < 0.001$ with logged
375 significantly to other plots in Tukey post-hoc test). This is surprising considering that regrowth
376 from clear felling could be considered a greater disturbance than selective logging, and that the
377 secondary plot contains *c.* 68 % of the intact plot biomass (Marchiori et al. 2016). This shows
378 that despite recovery of some characteristics (e.g. biomass), logged forest can still show
379 structural differences long after the logging event. Further, despite the difference in biomass
380 between the secondary and intact plots, the conditions for the understory may be quite similar.
381 Whilst logged forests will have a composition more similar to intact forest than secondary forest
382 (Gibson et al. 2011), the mid-canopy light conditions can be brighter and may be less conducive
383 to the growth of shade tolerant species than the darker mid-canopy of a recovering secondary
384 forest. Further understanding is needed on patterns of structural forest recovery after disturbance
385 and the consequences for the vertical light environment and tree growth.

386

387 To quantitatively compare light profiles between plots we estimated the extinction coefficient
388 (k_z) of light attenuation with canopy height (using only the profile data at and below rapid light

389 attenuation) and with canopy depth (k_d , using only the profile data from the canopy top to the
390 mean tree height) (Table 2, Fig. 3). The height-based extinction coefficient increased along the
391 disturbance gradient, intact-K < intact-M < logged < secondary < fragment-C < fragment-L, and
392 from examination of the 95% CI around k_z estimates, the extinction coefficients varied
393 significantly between all plots except intact-M and logged. The variance explained (R^2) by k_z for
394 the logged plot was low compared to the other plots due the inversion section of the logged
395 profile. Results based on k_d were similar to k_z , but without significant differences in k_d between
396 logged, secondary, and fragment-C. Both k_z and k_d were significantly negatively correlated with
397 canopy height (Pearson's correlation, $k_z - r = -0.98$, $p < 0.001$, $k_d - r = -0.88$, $p = 0.02$, Table 2).
398 This reflects the fact that % Transmission at the understory is low at all sites, but the canopy
399 heights are quite different; at the lower canopy forests a similar total amount of light is absorbed
400 to tall forests, but over a shorter vertical distance and hence k_z and k_d are higher. This may
401 indicate that many small dense crowns can absorb a similar amount of light to fewer large but
402 sparse canopies. K_d is probably a better descriptor of differences in light extinction between sites
403 than k_z because it includes all data-points from the top of the canopy.

404

405 To compare with data typically reported in other studies, we present the % Transmission at 1 m
406 above the ground in each plot (Table 2). The intact and secondary plots show low transmission,
407 with higher transmission in the logged and fragment plots. The differences between plots are
408 significant (Anova, $F=3.2$, $df=5$, $p=0.013$), however, only intact-K and fragment-L were
409 significantly different in a post-hoc test (Tukey, $p=0.035$). The lack of significant differences is
410 partly a result of high variance within plots, but does highlight that light measurements of the
411 understory cannot necessarily inform about the light environment above that sample point. For

412 example, even with a similar LAI below the canopy, the light profiles of two Amazonian forests
413 showed different patterns (Stark et al. 2012).

414

415 *Comparison of profiles from PAR sensors and hemispherical images*

416 Transmission as estimated from the PAR sensors and the vertical profiles of hemispherical
417 photos show good agreement (Fig. 2, Appendix S1: Fig. S4, Fig. 4). The R^2 of the relationship
418 between % transmission as measured with the PAR sensors and estimated from the
419 hemispherical images was 0.59 (Fig. 4). Of the 44 individual samples that had both sensor and
420 image profiles, the sensor and image transmission values were significantly correlated in 25
421 (Appendix S1: Fig. S4). Those that were not significantly correlated typically had few images
422 and/or showed little within profile variation. Even for those that were not correlated, the
423 transmission values were similar.

424

425 We believe this is the first study to estimate forest vertical light environments using profiles of
426 hemispherical images. Accessing the forest canopy is prohibitively difficult, and hence there are
427 few data on vertical patterns of canopy structure and light (Parker 1995). Previous attempts (in
428 temperate and boreal regions) have typically used cameras mounted on telescoping poles that can
429 only reach limited heights (e.g. 16 m, Wang et al. 1992; 10 m, Zhu et al. 2003; 6.8 m, Domke et
430 al. 2007), or from a single sample point using a tower (Strachan & McCaughey 1996). Recent
431 work has shown such knowledge can aid understanding of tropical forest dynamics (Stark et al.
432 2012, 2015), and light interception is a key aspect of vegetation models, from individual-based
433 forest simulators to dynamic global vegetation models. Whilst the burgeoning field of forest
434 canopy science (Nadkarni et al. 2011) will no doubt continue to be influenced by the high

435 resolution data available from LiDAR, such technology is still expensive and intensive data
436 processing and analysis is required to determine light environments from it. The method we
437 developed during this study enables rapid estimation of vertical light profiles from the ground
438 that can be repeated within and between sites to encompass spatial heterogeneity. The method is
439 inexpensive - the camera and lens used here costing around £1000 (less than the data loggers
440 required for the PAR sensors) – and the equipment is readily available. This could be a very
441 useful method to extend our understanding of vertical profiles of light (or leaf area) from more
442 locations, either in its own right or to compliment LiDAR-based data acquisition.

443

444 *Conclusions*

445 This study has measured patterns of vertical light penetration along a disturbance gradient in the
446 biodiversity hotspot of the Atlantic forest. Our results show that there is spatial variation in
447 vertical light patterns both within (Fig. 2) and between plots with different disturbance histories
448 (Fig. 3). Logging in particular has an impact on vertical light patterns, with greater within plot
449 heterogeneity and inversions in the profile due to lateral light from upper canopy gaps. This
450 pattern is still present despite 40 years of recovery from the logging event. We show that despite
451 similarities in transmission to the forest floor across all disturbances there are differences in
452 vertical structure and light extinction (Table 2) that may influence the light availability and hence
453 growth of mid-canopy trees. We also show the importance of non-tree life forms (e.g. lianas) for
454 light transmission and tree productivity in forest fragments. Finally, we recommend the rapid and
455 inexpensive methodology using hemispherical photographs for the characterization of forest
456 vertical light regimes, which are rarely measured.

457

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471

472 Data availability

473 The data is publicly available through deposit to NERC's Environmental Information Data
474 Centre (EIDC, Fauset et al. 2017).

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772 Tables

773 Table 1. Details of study plots.

Plot name	Plot code	Latitude/Longitude (decimal degrees)	Plot area (ha)	Fragment area (ha)	No. profile samples	No. hemispherical image profile samples	Dates of data collection (DD/MM, all 2015)
Intact-K	NSV-01	23.326 S / 45.068 W	1	Continuous	12	12	26/10 – 05/11
Intact-M	NSV-02	23.328 S / 45.073 W	1	Continuous	12	5	29/04 – 06/05
Logged	NSV-04	23.327 S / 45.076 W	1	Continuous	11	0	05/03 – 13/03; 28/04 – 29/04
Secondary	NSV-05	23.325 S / 45.094 W	1	Continuous	10	4	06/05 – 07/05; 20/05 – 21/05; 18/06 – 25/06
Fragment-C	SDM-11 / SDM-12	23.276 S / 45.241 W	2 x 0.25	12.2	12	12	14/10 – 22/10
Fragment-L	SDM-17 / SDM-18	23.100 S / 45.183 W	2 x 0.25	60.2	12	11	29/06 – 04/07

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775 Table 2. Metrics of the light environment in plots along a degradation gradient.

Plot	% Transmission at 1 m (mean \pm sd)	$k_z \pm 95\%$ CI (R^2)	$k_d \pm 95\%$ CI (R^2)	Max. sample tree height (m)	Mean sample tree height (m)
Intact-K	2.5 \pm 1.7	0.190 \pm 0.002 (0.98)	0.219 \pm 0.012 (0.98)	28	23.1
Intact-M	3.8 \pm 2.1	0.208 \pm 0.004 (0.96)	0.194 \pm 0.013 (0.98)	26	21.3
Logged	6.2 \pm 6.2	0.213 \pm 0.010 (0.85)	0.269 \pm 0.038 (0.89)	27	20.2
Secondary	2.4 \pm 2.0 [†]	0.246 \pm 0.004 (0.98)	0.265 \pm 0.007 (0.99)	25	19.2
Fragment-C	5.8 \pm 3.0	0.329 \pm 0.014 (0.92)	0.290 \pm 0.023 (0.98)	20	14.6
Fragment-L	7.5 \pm 5.7	0.474 \pm 0.019 (0.95)	0.653 \pm 0.035 (0.99)	17	10.5

776 [†] One value was excluded from the secondary forest mean % transmission at 1m as an outlier
777 which had been extrapolated from a relatively high (4m) lowest measurement (profile secondary-
778 8).

779

780

781 Figure Legends

782

783 Figure 1. Schematic and photograph of support structure for PAR sensors. Each structure is 1m
784 in length.

785

786 Figure 2. Example light profiles from each plot. Closed points - % transmission measured using
787 PAR sensors, grey – interpolated or extrapolated data points, open blue points - % transmission
788 estimated from hemispherical images (no profiles from hemispherical images were available
789 from the logged plot), red line – height of sample tree. Lower panels refer to the same plot as the
790 upper panel.

791

792 Figure 3. Observed mean light profiles with height (left panel) and depth below the canopy (right
793 panel) for forest plots along a disturbance gradient. Open circles represent data points where 3 or
794 more subplot profile measurements are based on interpolations or extrapolations due to
795 estimation of the top or bottom sections of the profiles. Dashed lines show standard deviation
796 between observed transmission values of different samples within the plot. Purple line -
797 extinction coefficient fit to mean light profile using height above the ground. Green line -
798 extinction coefficient fit to mean light profile using depth from top of canopy. Middle panels
799 show histograms of the sample tree heights within each plot.

800

801 Figure 4. Relationship between % Transmission measured from PAR sensors and estimated from
802 hemispherical images. Grey line – $y=x$, black dashed line – regression line.