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21 **Abstract:**

- 22 **1.** Despite ambitious, international forest landscape restoration targets, few forest
23 restoration approaches provide both ecologically sound and financially-viable
24 solutions for achieving the spatial scale proposed. One potential revenue source for
25 restoration is selective harvesting of timber, a product for which there is a clear
26 global market and increasing demand. Although the use of commercially valuable
27 exotic trees may attract farmers to restoration, it can be a major concern for
28 ecologists.
- 29 **2.** Here, we present results collected over 7 years from experimental studies at three
30 sites across the Brazilian Atlantic Forest to assess the impacts of incorporating
31 exotic eucalypts as a transitional stage in tropical forest restoration on aboveground
32 biomass accumulation, native woody species regeneration, and financial viability. .
- 33 **3.** Biomass accumulation was nine times greater in mixed eucalypt-native species
34 plantations than native only plantings due to fast eucalypt growth. Nonetheless, the
35 growth of native non-pioneer trees was not affected or only slightly reduced by
36 eucalypts prior to logging.
- 37 **4.** Eucalypts did not negatively affect the natural regeneration of native woody species
38 before or after eucalypt logging. Canopy cover regrew quickly but was slightly
39 lower a year following logging in mixed eucalypt-native species plantations.
40 Natural regeneration richness and planted non-pioneer growth were similar across
41 treatments in the post-logging period. We found higher variation of biomass
42 accumulation and native species regeneration among sites than between plantation
43 types within sites.

- 44 5. The income obtained from eucalypt wood production offset 44-75% of restoration
45 implementation costs.
- 46 6. *Synthesis and applications.* Many of the negative effects attributed to eucalypts on
47 the growth and natural regeneration of native trees depend on features of the
48 production system, landscape structure, soil, and climate in which they are grown,
49 rather than the effects of eucalypts *per se*. In Brazil's Atlantic Forest region, exotic
50 eucalypts can become important allies of tropical forest restoration, and their use
51 and investment opportunities should be considered within the portfolio of options
52 supported by public and private funding and policies.

53

54 **Keywords:** Atlantic Forest; ecological restoration; *Eucalyptus*; forest and landscape
55 restoration; large-scale restoration; natural regeneration; restoration costs; restoration
56 economy; selective harvesting; tropical forestry

57

58 **Introduction**

59 Tropical forest restoration has emerged as a promising intervention to mitigate climate
60 change, biodiversity loss, and improve human wellbeing in regions of the planet where
61 high endemic species richness coincides with widespread deforestation and forest
62 fragmentation (Holl 2017). Ambitious restoration targets have been set for tens to
63 hundreds of millions of hectares in tropical forest regions at the national, regional, and
64 international scales (e.g. Bonn Challenge, Initiative 20 × 20 in Latin America, Atlantic
65 Forest Restoration Pact in Brazil; Chazdon *et al.* 2017). But the high costs of forest
66 landscape restoration present a major obstacle for widescale adoption. For example, the
67 implementation phase alone can cost upwards of US\$3,700 per hectare in Brazil (Molin

68 *et al.* 2018), and international financing for such efforts is limited compared to the large
69 area proposed for restoration (12 M ha in Brazil alone). Restoring tropical forests
70 requires more than just compensating landowners for the use of the land. It demands
71 substantial investments in the implementation, maintenance, and long-term protection
72 and monitoring of recovering forests (Brancalion *et al.* 2017; Reid *et al.* 2018). Hence,
73 tropical countries need to develop innovative, financially-viable approaches to forest
74 restoration that are not heavily dependent on external aid that can stimulate large-scale
75 application to reach scale (Ding *et al.* 2017).

76

77 One potential revenue source for restoration is selective harvesting of timber, a product
78 for which there is a clear global market and increasing demand (Putz *et al.* 2012). From
79 an ecological perspective, forest restoration projects should prioritize planting native
80 tree species. However, fast-growing, exotic species comprise a potential alternative, if
81 they can help offset planting costs, do not inhibit the recolonization and growth of
82 native species, and speed up the recovery of forest functions (Ashton *et al.* 1997; Lamb,
83 Erskine & Parrotta 2005; Catterall 2016). Extensive production knowledge and
84 established timber markets for certain exotic tree species may transform restoration
85 plantings into a profitable activity and create investment opportunities (Brancalion *et al.*
86 2012; Grossman 2015; Payn *et al.* 2015). Several studies have found abundant and
87 diverse regeneration of native woody species in the understory of commercial tree
88 plantations across the global tropics (e.g. Brockerhoff *et al.* 2013; Pryde *et al.* 2015; Wu
89 *et al.* 2015), and highlight the potential of timber plantations to promote large-scale
90 forest restoration (Lugo 1997; Parrotta, Turnbull & Jones 1997). However, we are not
91 aware of any controlled or replicated experiments that rigorously assess the ecological
92 and economic outcomes of interplanting commercial exotic species with a diverse suite

93 of native species to facilitate regeneration of a diversity of tropical forest species and
94 offset restoration implementation costs by harvesting exotic planted trees.
95

96 Exotic eucalypts, planted for wood pulp and timber, are ubiquitous in tropical regions,
97 and currently cover over 20 million hectares globally. Only nine out of >700 *Eucalyptus*
98 and *Corymbia* species (hereafter referred to as “eucalypts”) comprise >90% of the
99 global planted area (Stanturf *et al.* 2013). The prominent environmental concerns
100 associated with the large plantation area and ecological characteristics of exotic
101 eucalypts have motivated several studies to assess their biodiversity value, allelopathic
102 effects, water consumption, and potential for invading unplanted areas (Bremer &
103 Farley 2010; Stanturf *et al.* 2013; Becerra *et al.* 2017). The effects of eucalypts vary,
104 however, with regional climate, previous land use, and plantation management practices
105 (Brockerhoff *et al.* 2013).
106

107 Eucalypts are grown in Brazil mostly for pulp, but also for round logs, sawn lumber,
108 firewood, fencing poles, and oil (IBA 2018). Such flexible uses and high productivity
109 (Brazil’s average: 35 m³ ha⁻¹ yr⁻¹, but reaching >60 m³ ha⁻¹ yr⁻¹ in some regions) make
110 eucalypts popular commercial trees for farmers (Goncalves *et al.* 2013); hence,
111 eucalypts comprise 71% of tree plantation area in Brazil (5.7 Mha, IBA 2018) and are
112 widely used in plantations throughout Latin America (Geary 2001; Salas *et al.* 2016).
113 Most of these plantations have been intensively managed in short rotations (~5 yr) and
114 as extensive monoculture areas, which have prevented the natural regeneration of native
115 woody species and resulted in so-called “green deserts” (Bremer & Farley 2010).
116 However, less intensively managed and abandoned eucalypt plantations in many regions

117 host a high diversity of plants and birds (Silva-Junior, Scarano & Cardel 1995;
118 Marsden, Whiffin & Galetti 2001; Lopes *et al.* 2015; César *et al.* 2017).
119
120 Forest restoration projects in Atlantic forest region of Brazil mostly plant a high
121 diversity of native tree species (Rodrigues *et al.* 2011; Brancalion *et al.* 2018), but the
122 Native Vegetation Protection Law of 2012, allows for intercropping exotic,
123 commercially-valuable tree species with native species in restoration projects to meet
124 restoration requirements . The justification for this legislative change from the earlier
125 1965 Forest Code was the need to transform restoration into a financially-viable land
126 use (Brancalion *et al.* 2012), which compensates farmers for the opportunity costs of
127 foregone agricultural land use. Here, we draw on results from experimental studies at
128 three sites across the Brazilian Atlantic Forest to rigorously assess the impacts of
129 incorporating exotic eucalypts as a transitional stage in tropical forest restoration on
130 aboveground biomass accumulation, native woody species regeneration, and costs. This
131 information is important to evaluate the ecological and financial viability of this novel
132 legal norm and its potential for dissemination to other global regions to leverage tropical
133 forest restoration.

134

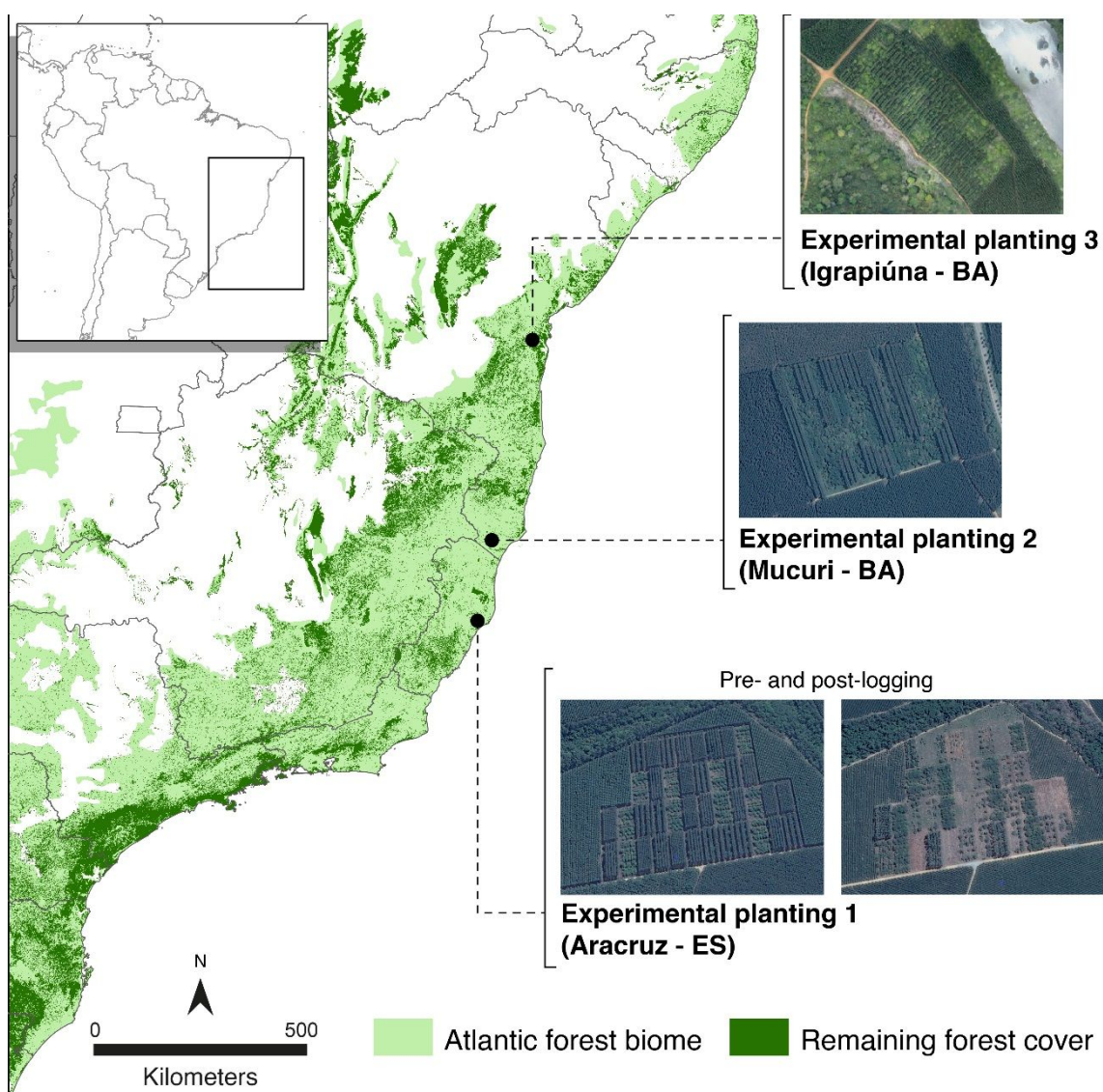
135 **Materials and Methods**

136 ***Experimental sites***

137 We established experimental plantings in three municipalities distributed across the
138 eastern portion of the Atlantic Forest (Site 1: Aracruz-Espírito Santo, Site 2: Mucuri-
139 Bahia, and Site 3: Igrapiúna-Bahia; **Table S1, Fig. 1**) as a joint effort of the Atlantic
140 Forest Restoration Pact, two eucalypt pulp companies, and one conservation NGO to
141 develop new forest restoration models with the objective of offsetting implementation

142 costs and providing income to farmers. We established and compared two experimental
143 treatments at each site: i) diverse plantations of native species: 23-30 species of native
144 non-pioneer trees intercropped with 9-10 species of native pioneer trees (hereafter
145 “native” treatment); ii) mixed plantations of native species and eucalypts: the same 23-
146 30 species of native non-pioneer trees intercropped with eucalypts in equal proportions
147 of eucalypt and native non-pioneer species (“mixed” treatment; **Table S1**). Native non-
148 pioneer trees were mostly composed of valuable timber species, which could potentially
149 be harvested by farmers in long rotation cycles to further contribute to the financial
150 viability of restoration. We employed a random block design with five (site 1), four (site
151 2) and six (site 3) blocks (**Table S1**). Sites 1 and 2 were planted at 3×3 m spacing
152 ($1,111$ trees ha^{-1} ; plot size $2,160$ m^2) and site 3 at 3×2 m spacing ($1,666$ trees ha^{-1} ; plot
153 size $1,080$ m^2); in all sites, we intercropped two consecutive lines of each group of
154 species (*i.e.*, eucalypts, native pioneers, and native non-pioneers).

155



156

157 Figure 1. Study sites within the Atlantic Forest of Brazil. Black lines in Atlantic Forest
 158 map indicate state boundaries. See Table S1 for biophysical and experimental site
 159 details. Other treatments were tested in these sites and can be seen in the images (e.g.
 160 eucalypt monocultures, intercropping eucalypts and native species in single lines), but
 161 these treatments are not discussed in this paper.

162

163 We logged eucalypt trees in all mixed plantation plots at site 1 with a harvester and
 164 forwarder after 57 months, and logged all eucalypt trees in half of these plots (six
 165 harvested and six unharvested) in site 3 with chainsaw and animal traction after 45
 166 months; mixed plantations have not yet been harvested at site 2 because it is being

167 managed for a longer rotation cycle. We left unharvested plots at site 3 to compare the
168 longer-term impacts of maintaining versus logging eucalypts on the further
169 development of planted native trees and natural regeneration. We employed a reduced
170 impact logging approach in order to minimize logging impacts on planted native trees
171 and natural regeneration.

172

173 ***Data collection***

174 *Aboveground biomass accumulation and growth of planted non-pioneer trees*

175 We measured the DBH and height of all planted native trees and eucalypts in the
176 effective area of experimental plots in site 1 (pre-logging: 38, 51 and 57 months; post-
177 logging: 83 months), site 2 (pre-logging: 48 months) and site 3 (pre-logging: 31 and 43
178 months; post-logging: 53, 60, and 84 months; **Fig. S1**). We estimated native tree
179 aboveground biomass (AGB) 4-5 yr after planting using an equation developed for 5-yr
180 old restoration plantings in the Atlantic Forest (Ferez *et al.* 2015), and calculated
181 eucalypt AGB with an equation developed specifically for eucalypt stands in the study
182 region (Rocha 2014). In the native plantations, we calculated the AGB of pioneer and
183 non-pioneer trees separately in order to assess the differential impact of eucalypts and
184 native pioneers on the growth of native non-pioneer trees.

185

186 *Regeneration environment and woody species regeneration*

187 We assessed the light environment and invasive grass cover in the plantation understory
188 right before (Site 1: 57 months; Site 3: 43 months) eucalypt logging, and the light
189 environment immediately following and 7 (Site 1) to 12 (Site 3) months after eucalypt
190 logging (**Fig. S1**). We did not take natural regeneration measurements in site 2 because
191 the company in charge of maintaining the site inadvertently sprayed glyphosate in the

192 plantation understory to control grasses, a standard practice in eucalypt plantations,
193 which also killed native regenerating trees; moreover, since the site is being managed on
194 a longer-term rotation, we could not take post-harvest natural regeneration data.

195

196 We estimated light availability using two methods due to different weather conditions at
197 the sites. In site 1, where open sky days predominated during the data collection period,
198 we measured photosynthetically active radiation from 11 to 13h in the plantation
199 understory and outside the plantation with a ceptometer AccuPAR LP-80 (Decagon
200 Devices Inc., 1999) and calculated the leaf area index (LAI). In site 3, where cloudy
201 days predominated during the data collection period, we measured the red:far red ratio
202 in plantation understory with a Skye SKR 110 sensor (Skye Instruments), which
203 captures radiation between 660 and 730 nm wavelengths and does not require
204 measurements in open areas; lower red:far red ratio indicates reduced diffuse
205 transmittance through a more closed canopy (Capers & Chazdon 2004). We regularly
206 distributed ten (Site 1) and six (Site 3) 2 × 2 m quadrat subplots in each experimental
207 plot and visually estimated invasive grass cover (mostly *Urochloa decumbens* (Stapf
208 R.D. Webster) according to five classes (0, 25, 50, 75, and 100% approximate cover).
209 We then identified and quantified all spontaneously regenerating tree species
210 individuals (height ≥50 cm) growing within the subplots used for grass cover
211 measurements, prior to logging (Site 1: 57 months; Site 3: 43 months) and 3-4 years
212 after post logging.

213

214 *Logging impacts on planted non-pioneer trees*

215 We evaluated the damages of eucalypt logging on planted non-pioneer species in Sites 1
216 and 3 right after logging based on a methodology adapted from Sist and Nguyen-Thé

217 (2002), through which trees were classified as with or without the trunk broken, and
218 with or without damages (damages on tree crown, trunk/bark, and/or bole inclination).
219 We assessed if broken or damaged trees survived seven months after logging, based on
220 the presence of living leaves of new sprouts.

221

222 ***Data analysis***

223 *Aboveground biomass accumulation and growth of planted non-pioneer trees*

224 We compared the total AGB and the AGB of non-pioneer species between mixed and
225 native plantations at the pre-harvesting stage 4-5 yr after planting at all three sites. AGB
226 stocks were compared by independent t-tests as data showed normality and
227 homoscedasticity. To compare the growth of planted non-pioneer trees with and without
228 eucalypts, and before and after eucalypt logging, we used linear mixed-models
229 following a model-building approach in order to detect and prevent heteroscedasticity
230 and dependency (Zuur *et al.* 2009). Models were fitted in R using *lme* function in the
231 *nlme* package (Pinheiro *et al.* 2018), using *varPower* and *corARI* model options when
232 necessary. We used basal area of non-pioneer trees as the response variable, time and
233 treatment as fixed factors and time factor and individual identity as random variables in
234 our mixed models (for more details, see Annex 1). Then, we analyzed how non-pioneer
235 trees responded after eucalypt logging at two sites by comparing plots where eucalypts
236 were logged and areas where non-pioneer trees were growing with native pioneer trees.
237 We compared the basal area increment (difference between the basal area of the pre-
238 and post-logging inventories) between treatments with Welch t-test, since data showed
239 normal distribution but unequal variances.

240

241 *Regeneration environment and woody species regeneration*

242 The leaf area index (Site 1) and red:far red ratio (Site 3) data were compared between
243 treatments and along time by mixed model approach and paired t-tests. As consequence
244 of the frequent number of subplots with zero values of grass cover, we employed a
245 Zero-Inflated Mixed Model approach (Zuur *et al.* 2009) with the function *zeroinfl*
246 (Zeileis *et al.*, 2008) of *pscl* package (Jackman 2010), using the treatments and the light
247 environment variable as fixed factors in the models. We compared the rarefied species
248 richness and species composition similarity of saplings regenerating in the understories
249 of native and mixed plantations, prior to and after eucalypt logging (Fig. S1). In site 3,
250 we also included unlogged plots of mixed plantations, which allowed us to infer the
251 persistence impacts of eucalypts on native species regeneration.

252

253 We compared native species richness through rarefaction curves based on sample-sizes
254 with 95% confidence intervals using the R package *iNEXT* (Hsieh, Ma & Chao 2016),
255 and composition similarity according to the Chao-Jaccard similarity index. We
256 compared the abundance of regenerating native species through Poisson Generalized
257 Linear Mixed Model (GLMM), following a model construction approach (Zuur *et al.*
258 2009), using *glmer* function from *lme4* package (Bates *et al.* 2015) and post hoc test
259 with *lsmeans* package (Lenth 2016), where time and treatment were fixed factors and
260 plot ID as random factor (for more details, see Annex 1).

261

262 *Financial calculations*

263 We quantified plantation implementation (site preparation, seedling acquisition,
264 fencing, tree planting) and maintenance (weeding, control of leaf-cutter ants, and
265 sequential fertilization) costs based on the prices of services and materials supplied by
266 professional restoration companies near Site 1. We assumed the costs of Site 1 Aracruz

267 region to be the same as for the other sites, an assumption justified by a large-scale
268 study showing similar costs of restoration management practices across in Brazil. We
269 quantified the differential seedling costs of the two treatments; but we did not quantify
270 the labor and inputs costs of mixed and native plantations separately, although mixed
271 plantings should have lower weeding costs due to faster canopy cover.

272

273 We applied a timber price of harvested trees (US\$ 28.41 m⁻³) and discounted logging
274 and transport costs (US\$ 6.35 m⁻³), for the Site 1 region (Silva 2012; Brazilian-Tree-
275 Industry 2015), to calculate total revenue. Timber production was evaluated based on
276 direct harvesting of eucalypts in two sites (Site 1: 100.38 m³ ha⁻¹, Site 3: 174.08 m³ ha⁻¹)
277 and estimated in Site 2 based on the relationship between basal area and wood harvested
278 obtained in Site 1 and applied to the forest inventory of Site 2 (93.72 m³ ha⁻¹). The
279 revenue obtained from eucalypt logging in experimental plantings was calculated based
280 on the Net Present Value, assuming the financial parameters of: i) R\$1.00=US\$0.3131;
281 ii) inflation of 1.06 (2011-2014) and 1.11 (2015), based on the Broad National
282 Consumer Price Index - IPCA (www.bcb.gov.br/pec/Indeco/Ingl/indecoi.asp); and iii)
283 basic interest rate of 11% for 2014 (www.bcb.gov.br/Pec/Copom/Port/taxaSelic.asp).

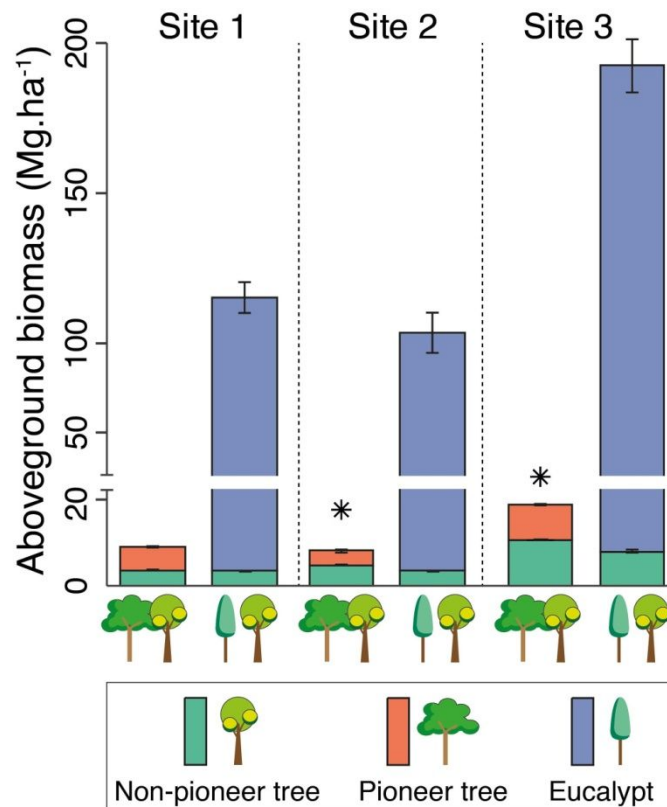
284

285 **Results**

286 *Aboveground biomass accumulation and growth of planted trees*

287 Aboveground biomass of mixed plantations was approximately nine times greater than
288 native plantations, mostly as consequence of the rapid growth of eucalypts (**Fig. 2**).
289 These results were accompanied by a slight, but significant, reduction in the AGB of
290 non-native pioneer trees in two experimental sites (**Fig. 2**).

291



292

293 Figure 2. Aboveground biomass (AGB) accumulation in experimental restoration native
 294 and mixed plantings. Total AGB was higher in mixed plantations with eucalypts in all
 295 sites, and asterisks indicate that AGB of non-pioneer trees was significantly higher
 296 without eucalypts (t-tests, $p < 0.05$) in two sites. Error bars represent 95% confidence
 297 intervals.

298

299 In Site 1, the basal area of non-pioneer species showed similar increases across
 300 treatments over time ($F_{1,58} = 3.33$, $p = 0.07$; treatment \times time interaction $F_{1,58} = 5.31$, $p =$
 301 0.02) so basal area in both native and mixed plantations was similar at the last inventory
 302 ($t_{11} = 0.672$, $p = 0.98$; **Fig. 3A**; **Table S2**). In Site 3, the basal area of non-pioneer
 303 species increased faster in native plantations during the experiment (slope estimate \pm
 304 SE: native = 0.102 ± 0.03 ; mixed logged = 0.042 ± 0.02 , and mixed unlogged = $0.044 \pm$
 305 0.02 ; treatment \times time interaction $F_{1,46} = 8.94$, $p < 0.005$; **Fig. 3B**), which resulted in a
 306 94% higher basal area seven years after planting in the native compared to mixed

315 *Logging impacts on planted non-pioneer trees*

316 Logging impacts were higher in site 3 (45.4% of non-pioneer trees), where eucalypt was
 317 logged with chainsaw, than in site 1 (13.2%), where logging was done using a harvester
 318 machine (**Table 1**). Nonetheless, mortality was very low in both sites after seven
 319 months (**Table 1**), since most broken and damaged trees resprouted following logging
 320 damage.

321

322 Table 1. Impacts of eucalypt logging on planted non-pioneer trees in mixed plantations,
 323 and mortality of impacted trees seven months after harvesting

Study Area	Broken trees (%)	Broken trees mortality (%) ¹	Damaged trees (%)	Damaged trees mortality (%) ¹
1	0.0 ± 0.0	0.0 ± 0.0	13.2 ± 1.8	0.0 ± 0.0
3	16.9 ± 3.4	2.6 ± 0.5	45.4 ± 4.8	0.7 ± 0.5

324 ¹percentage of dead trees in relation to the total number of alive trees before logging

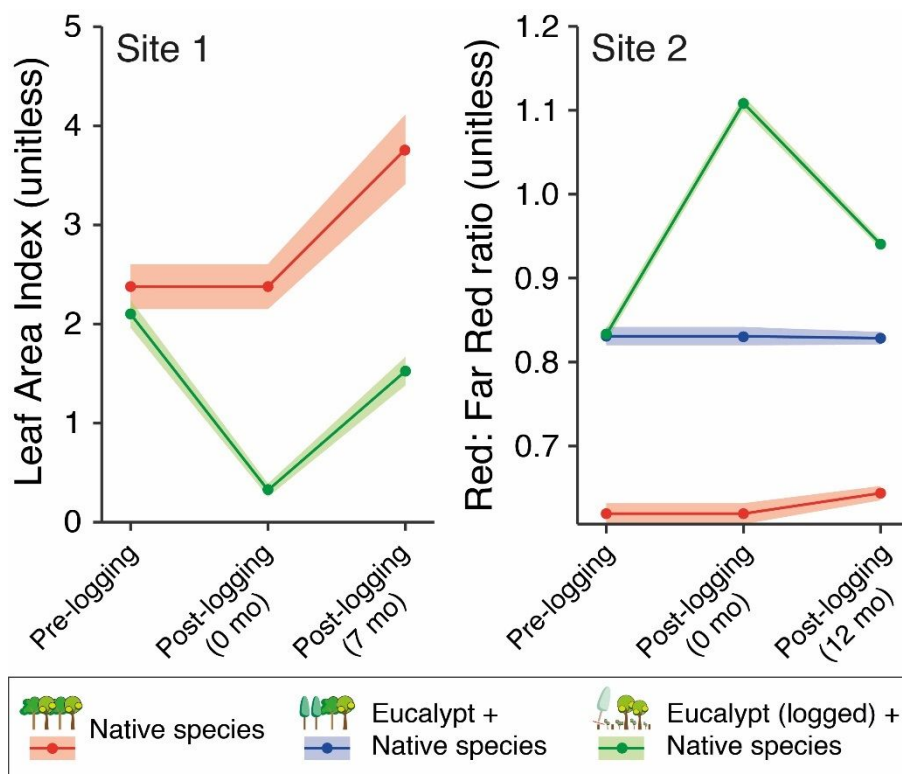
325

326 *Regeneration environment*

327 The leaf area index of native and mixed plantations was similar in site 1 prior to logging
 328 ($t_{7,1} = 1.03$; $p = 0.38$; **Fig. 4A**). Eucalypt logging reduced LAI by nearly a third in mixed
 329 plantations ($t_9 = 11.95$; $p < 0.001$; **Fig. 4A**), but the growth of the remaining planted and
 330 regenerating native trees more than tripled the LAI of logged plots and reached 84% of
 331 pre-logging values 7 months after logging (**Fig. 4A**). In site 3, red:far red ratio was
 332 lower (i.e. canopy cover was higher) in native plantations prior to logging ($F_{2,429} =$
 333 132.88 ; $p < 0.001$; **Fig. 4B, S2**). Eucalypt logging showed a similar trend in site 3 (~30%
 334 increase in red:far red ratio values; $t_{143} = 25.97$; $p < 0.001$; **Fig. 4B**). A year post logging,
 335 the remaining native trees had reached 85% of red:far red ratio values of unlogged
 336 mixed plots and 68% of native plantations values, yet logged mixed plots had the
 337 highest red:far red ratio values at this time ($F_{2,429} = 426.5$; $p < 0.0001$; **Fig. 4B**). Invasive

338 grass cover was low in both sites (Site 1: ~10%; Site 3: ~7%) and did not differ between
 339 treatments prior to logging (Site 1: $|Z| < 1.44$; Site 3: $|Z| < 0.53$; $p > 0.05$).

340



341

342 Figure 4. Temporal variation of light environment in the understory of experimental
 343 restoration plantings of native and mixed plantations, submitted or not to logging.

344 Shading represents 1 SE.

345

346 *Regeneration of native woody species*

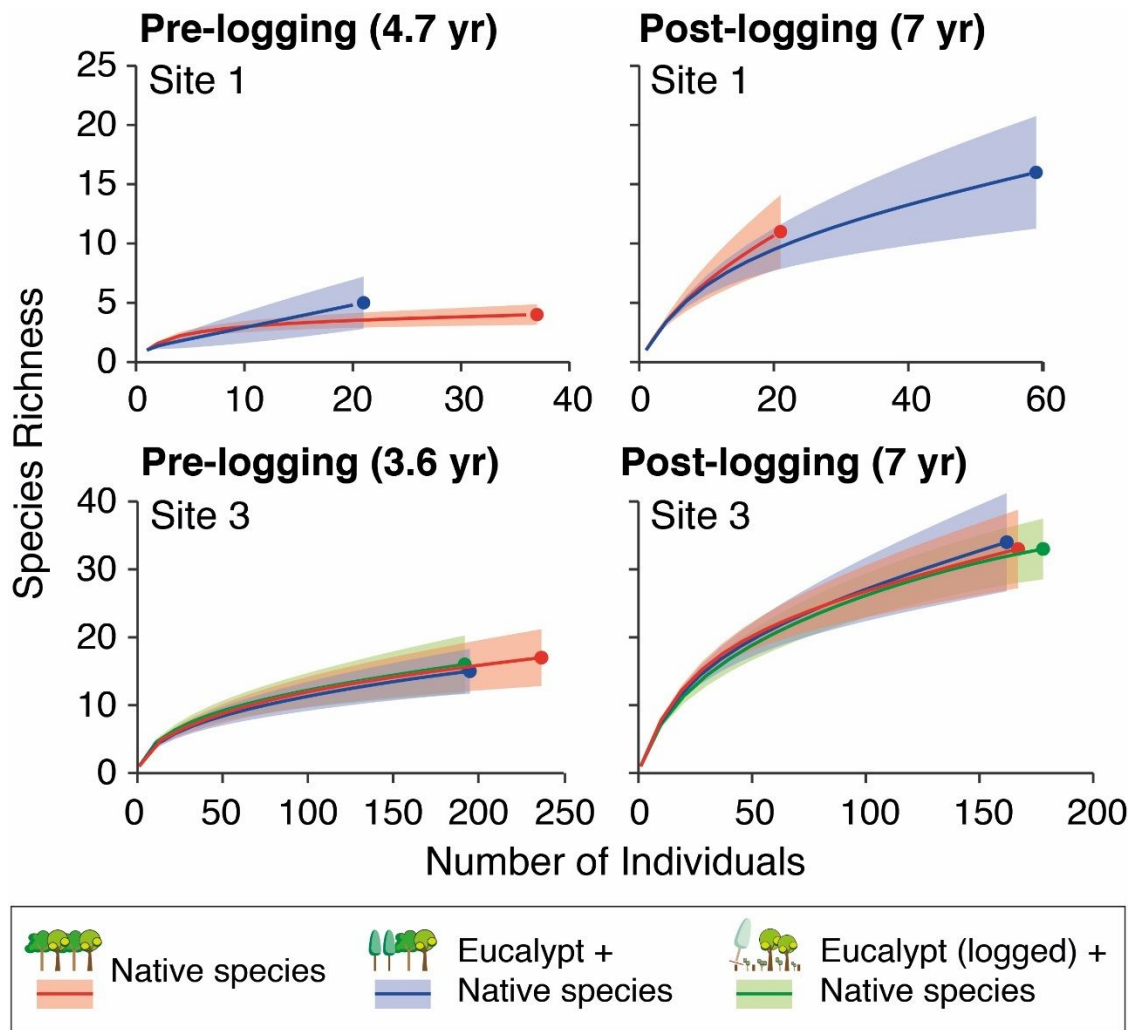
347 Rarefied species richness and composition of native woody species that colonized the
 348 understory of native and mixed plantations were similar in the pre-logging period (Site
 349 1: Chao-Jaccard similarity: 0.75; **Fig. 5A**; Site 3: Chao-Jaccard similarity: 0.95; **Fig.**
 350 **5B**) with twice as many species at site 3 compared to site 1. Rarefied species richness
 351 doubled and tripled in sites 1 and 3, respectively, in the post-logging period, but did not
 352 differ among plantation types within each site (**Fig. 5**). We did not observe a single

353 regenerating eucalypt seedling in either site pre- or post-logging. In site 1, the
354 abundance of regenerating native species was higher in native plantations in the pre-
355 logging period, but was similar at the post-logging period (Table S3), as consequence of
356 a slight abundance decrease in native plantations and increase in mixed plantations
357 between periods (slope estimate \pm SE: Site 1: native = -0.28 ± 0.25 ; mixed = 1.55
358 ± 0.24 ; treatment \times time interaction $|Z|=5.33$, $p < 0.001$; Table S3). In site 3, the
359 abundance of regenerating native species was similar in treatments in the pre-logging
360 period, but was higher in native plantations in the post-logging period, when logged and
361 unlogged plots did not differ (Table S3). We observed a slight increase in the abundance
362 of regenerating species in native plantations and a decrease in mixed plantations (native
363 = 0.06 ± 0.09 ; mixed logged = -0.35 ± 0.11 , and mixed unlogged = -0.29 ± 0.11 ;
364 treatment \times time interaction $|Z|_{\text{logged}} = 2.79$, $p = 0.005$, and $|Z|_{\text{unlogged}} = 2.42$, $p = 0.02$;
365 Table S3).

366

367

368



369

370 Figure 5. Rarefied species richness of naturally regenerating native woody species in
 371 native and mixed restoration plantings with or without eucalypt logging. Shading
 372 represents 95% confidence intervals.

373

374 *Financial assessment of eucalypt logging*

375 Wood production in mixed plantations with eucalypts helped to offset the high
 376 implementation and maintenance costs (\$3,360 ha⁻¹). Eucalypt harvesting in 4-5 yr old
 377 experimental plantings yielded 100 (Site 1), 94 (Site 2), and 174 m³ ha⁻¹ (Site 3) of
 378 roundwood for pulp, firewood or fencing poles (DBH 15-25 cm), compensating for 46.6
 379 (Site 1), 44.00 (Site 2), and 75.3% (site 3) of total restoration implementation costs 4-5
 380 years after planting (Table S4).

381

382 **Discussion**

383 Our results show that mixing plantations of eucalypts and native trees is a promising
384 restoration strategy to help offset restoration implementation costs without undermining
385 the ecological outcomes. The growth of native non-pioneer trees was not affected (1
386 site) or slightly reduced (2 sites) by eucalypts prior to logging despite the greatly
387 enhanced biomass production of mixed plantations. Moreover, the richness of
388 regenerating native woody species was not reduced by eucalypts either before or after
389 eucalypt logging, yet the abundance of regenerating native species was higher in native
390 plantations in sites 1 (pre-logging) and 3 (post-logging).

391

392 The most evident difference between native and mixed plantations was the short-term
393 difference in AGB accumulation. With nearly nine times higher AGB stocks prior to
394 logging, mixed plantations clearly demonstrated the value of integrating eucalypts as a
395 transitional phase in restoration if wood production is one of the expected outcomes
396 (Amazonas *et al.* 2017; Lamb 2018). The fact that the impressive biomass accumulation
397 of eucalypts did not strongly reduce the growth of planted native non-pioneer trees may
398 be due to the naturally slow growth of this group of species (Chazdon 2014) and their
399 adaptation to tolerate low to medium light conditions (Loik & Holl 1999). We lack
400 plantations of exclusively non-pioneer trees to disentangle competition in these systems.

401

402 We had anticipated that the fast growth of eucalypts would result in higher canopy
403 cover and consequently less grass cover than native plantations. In contrast, we found
404 the opposite result for canopy cover in one site and no difference in another, and no
405 impact on grass cover in either site. These unexpected results can be explained by the

406 contrasting architecture of the tree crowns of eucalypts and native species. The eucalypt
407 species used in the experimental plantations have monopodial branching, which
408 concentrate leaves at the top of plantation canopy and result in a leafless midstory
409 (Almeida *et al.* 2019). On the other hand, native plantations usually have branches and
410 leaves throughout all the forest vertical strata to maximize light absorption by species
411 with different ecophysiological behaviors and niche requirements (Sapijanskas *et al.*
412 2014). The shade levels in both plantations types appeared to be sufficiently high to
413 prevent grass regrowth in the understory, a major barrier for restoration success in the
414 Atlantic Forest region.

415

416 A valid concern about interplanting eucalypts with native species is that the impacts of
417 falling trees and dragging logs could largely destroy the native non-pioneer trees
418 interplanted with eucalypts and the abundant natural regeneration of the understory. In
419 fact, the visual impression right after logging was that all regenerating individuals were
420 destroyed in eucalypt planting lines, where logging impacts were concentrated (**Fig.**
421 **S3**). In site 3, nearly half of planted non-pioneer trees were damaged by logging; but
422 most broken trees resprouted and damaged trees survived seven months after logging,
423 resulting in negligible mortality levels. The species richness of regenerating woody
424 plants was similar between logged mixed plantations and native plantations a few years
425 after logging, but the abundance of regenerating individuals was reduced in both logged
426 and unlogged mixed plantations in site 3 compared to native plantations. We had
427 expected planted native non-pioneer trees would grow faster in the post-logging period,
428 given that seedling growth is commonly light limited in plantations (Paquette, Bouchard
429 & Cogliastro 2006) and tropical secondary forest (Chazdon *et al.* 1996), but growth
430 post-logging growth rates were similar in logged and unlogged treatments. In site 3, the

431 potential benefits of greater light availability may have been counterbalanced by the
432 higher levels of physical damage of logging to planted native non-pioneer trees.

433

434 The lack of differentiation of regenerating communities both in terms of species
435 richness and composition, may reflect the spatial proximity of the plots. Although we
436 used large experimental plots (2,160 and 1,080 m²), compared to those traditionally
437 used in restoration experiments (Shoo & Catterall 2013), seed dispersers may have been
438 attracted to the heterogeneous forest structure and abundant animal-dispersed trees of
439 the experimental site in general (Reid, Harris & Zahawi 2012). This local enhancement
440 of seed dispersal could mask the differential potential of native trees, especially of
441 pioneers, to attract seed dispersers, yet some studies have reported diverse bird
442 communities in the understory of abandoned eucalypt plantations in the Atlantic Forest
443 region (Marsden, Whiffin & Galetti 2001; Lopes *et al.* 2015).

444

445 Differences in both aboveground biomass accumulation and natural regeneration were
446 much more strongly affected by site factors than by planting treatment. The nearly
447 three-fold higher tree growth rates at site 3 likely reflect more favorable soil and climate
448 conditions (site 3 vs. site 1: soil sum of bases: 23.81 vs. 1.93 mmol_c.dm⁻³; clay content:
449 71.4 vs. 20.9%; annual rainfall: 2,191 vs. 1,412 mm; **Table S1**) and less intensive prior
450 land use (extensive pasture vs. intensive eucalypt plantation). The greater species
451 richness of recruits in site 3 may be explained by those factors, as well as higher
452 landscape forest cover (20.8% vs. 6.3%) than site 1. All three factors have been
453 demonstrated to affect the rate of tropical forest recovery in prior studies (reviewed in
454 Holl 2007; Chazdon 2014).

455

456 Eucalypt allelopathic effects (Becerra *et al.* 2017), cases of invasion (Tererai *et al.*
457 2013), reduction in soil moisture (Robinson, Harper & Smettem 2006) and problems
458 with wildfires (Moreira & Pe'er 2018), have been reported predominantly in drier
459 climates. These do not seem to be similarly problematic issues in wetter tropical
460 regions, as suggested by our results and several previous studies in tropical regions that
461 found diverse and abundant regeneration of native species in the understory of eucalypt
462 plantations (e.g. Silva-Junior, Scarano & Cardel 1995; Bremer & Farley 2010; Pryde *et*
463 *al.* 2015). We did not find any evidence of natural recruitment of eucalypts in our plots.
464 Data from a related study at our sites (Amazonas *et al.* 2017) showed minimal
465 differences in soil volumetric water content in shallow soil layers (up to 1.3 m depth) of
466 ~4.5-yr native, mixed, and eucalypt monoculture plantations. This lack of difference in
467 soil water availability may be due to the fact that most native pioneer species also
468 require large amounts of water to sustain their fast growth (Filoso *et al.* 2017).

469

470 As expected, eucalypt logging resulted in a valuable contribution to offset ~45-75% of
471 restoration implementation and maintenance costs. Harvesting eucalypts or other
472 commercially valuable native or exotic trees in restoration could partially overcome the
473 financial barrier for adopting active restoration approaches, which can cost up to ten
474 times more than natural regeneration (Shoo *et al.* 2017), but are needed in many cases
475 due to low site resilience (Rodrigues *et al.* 2011; Shoo *et al.* 2016). Exotic eucalypts can
476 thus become important allies of tropical forest restoration, and their use should be
477 considered within the portfolio of options supported by public and private funding and
478 policies (Catterall 2016). Together, our results suggest eucalypt use as a transitional
479 stage in restoration has a neutral effect on natural regeneration and can help offset
480 restoration costs along with complementary strategies that aim to transform restoration

481 into a competitive land use, like payments for ecosystem services and harvesting
482 valuable native timber species in long rotations (Brancalion *et al.* 2017). Like any novel
483 restoration strategy, this approach must be considered in the context of the ecosystem
484 type and evaluated for localized positive and negative effects prior to large-scale
485 implementation.

486

487 **Data archive statement:** Our data is archived at GitHub
488 (<https://doi.org/10.5281/zenodo.2583906>).

489

490 **Author contributions:** P.H.S.B. conceived the idea, designed the study, and led the
491 writing. K.D.H. co-led the writing. P.H.S.B. and K.D.H. decided on statistical analysis
492 and J.M. conducted them. N.T.A., C.C.S., T.B.S., A.F.M., P.H.S.B., and R.R.R. planned
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494

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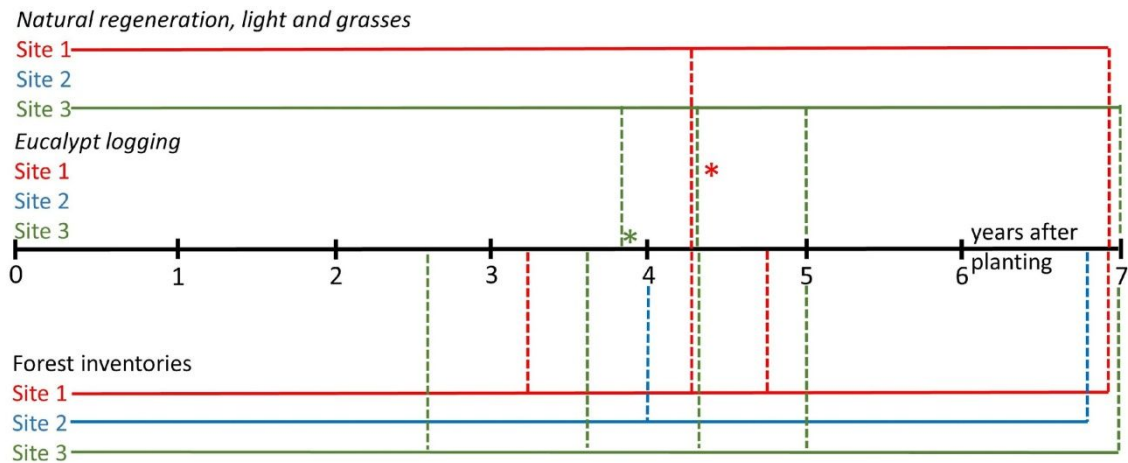


Figure S1. Timeline of interventions and data collection in the three experimental sites.



Fig. S2. Hemispheric photographs of the canopy of native (left) and mixed (right) plantations.



Fig. S3. Overview of the mixed plantation in Site 3 right after eucalypt logging.

Table S1: Biophysical and experimental characteristics of the study sites.

Characteristics	Experimental plantings		
	Aracruz Espírito Santo state	Mucuri Bahia state	Igrapiúna Bahia state
Coordinates	19°49'12"S, 40°16'22"W	18°05'09"S, 39°33'03"W	13°49'0"S, 39°9'0"W
Land tenure	Private	Private	Private
Altitude	41 m	78 m	121 m
Mean rainfall	1,412 mm	1,531 mm	2,191 mm
Mean temperature	23.4°C	23.9°C	25°C
Climate (Köppen classification)	Aw; dry cold winter and a hot wet summer	Af; no dry season	Af; no dry season
Drier period	Feb-Sep	Jan-Apr	Nov-Mar
Soils	Yellow Argisol (Ultisol); sandy/ clayey texture	Argisol; clayvey (40%)	Dystrophic Yellow-Red Oxisol; clayey
Cation Exchange Capacity (mmol _c .dm ⁻³)	2.16	1.83	58.64
Sum of Bases (mmol _c .dm ⁻³)	1.93	1.43	23.81
Clay (%)	20.9	17.2	71.4
Relief	Flat	Flat	Rounded hills with soft slopes
Native forest cover within a 5-km radius	6.3%	28.3%	20.8%
Experimental design	Random block design; 5 blocks	Random block design; 4 blocks	Random block design; 6 blocks
Treatments*	NE; NN; EE	NE; NN; EE	NE; NN
Date of plantation	July 2011	May 2012	June 2011
Plot size	2,160 m ²	2,160 m ²	1,080 m ²
Plot design	10 lines of 24 trees; two outer rows as border	10 lines of 24 trees; two outer lines as border	15 lines of 12 trees; one outer line as border
Plantation spacing	3×3 m	3×3 m	3×2 m
Number of seedlings within effective plot	120	120	130

Seedlings per hectare	1,111	1,111	1,667
Eucalypt planted	<i>E. grandis</i> × <i>E. urophylla</i>	<i>E. urophylla</i>	<i>E. grandis</i> × <i>E. urophylla</i>
Native pioneers	10 species	10 species	9 species
Native non-pioneer	30 species	28 species	23 species

* NE= native species + *Eucalyptus*; NN= native species + native pioneers; EE= *Eucalyptus* monoculture

Table S2 –Basal area mean of native non-pioneer species in the last inventory, with confidence limits obtained by a nonparametric bootstrap.

Site	Treatment	Mean basal area (m ² ha ⁻¹)	Minimum limit	Maximum limit
Site 1	Native	0.0221	0.0179	0.0265
	Mixed logged	0.0281	0.0187	0.0384
Site 3	Native	0.0120	0.00926	0.0153
	Mixed logged	0.00785	0.00624	0.00968
	Mixed unlogged	0.00781	0.00634	0.00959

Table S3. Abundance of regenerating native wood species per plot (mean and minimum – maximum confidence limits by nonparametric bootstrap, 95% confidence interval and 1000 bootstrap resamples).

Site	Treatment	Before logging (50 months)	After logging (83 months)
Site 1	Native	9.25 (7.0 - 11.8)	7 (4.8 - 9.8)
	Mixed logged	2.3 (1.6 - 3.1)	11 (5.3 - 17.7)
Site 3	Native	7.3 (4.6 - 10.6)	8.2 (6.1 - 10.4)
	Mixed logged	5.7 (4.1 - 7.4)	3.9 (3.0 - 4.9)
	Mixed unlogged	6.3 (4.5 - 8.2)	4.7 (3.9 - 5.6)

Table S4: Economic analysis of the potential of harvesting eucalypt timber (4-5 yr rotations) in mixed plantings with native trees to offset per hectare restoration implementation and maintenance costs in the Atlantic Forest of Brazil.

A. Traditional restoration plantings, without eucalypts							
Site	Year	Activity	Costs	Revenue	Present Value	Net Present Value	restoration costs offset
all	0	Site preparation	\$ -775	\$ -	\$ -775		
all	0	Planting	\$-1,034	\$ -	\$-1,034		
all	0	Maintenance	\$ -232	\$ -	\$ -232		
all	1	Maintenance	\$-1,023	\$ -	\$ -922		
all	2	Maintenance	\$ -310	\$ -	\$ -251		
all	3	Maintenance	\$ -122	\$ -	\$ -89		
all	4	Maintenance	\$ -50	\$ -	\$ -33		
all	5	Maintenance	\$ -40	\$ -	\$ -24		
all	5				\$ -	\$-3,360	0%
B. Mixed plantings of eucalypts and native trees							
Aracruz	Year	Activity	Costs	Revenue	Present Value	Net Present Value	restoration costs offset
Aracruz	0	Site preparation	\$ -775	\$ -	\$ -775		
Aracruz	0	Planting	\$ -928	\$ -	\$ -928		
Aracruz	0	Maintenance	\$ -232	\$ -	\$ -232		
Aracruz	1	Maintenance	\$-1,023	\$ -	\$ -922		
Aracruz	2	Maintenance	\$ -310	\$ -	\$ -251		
Aracruz	5	Logging and transport	\$ -638	\$ 2,852	\$ 1,314	\$-1,795	46.6%
Mucuri	0	Site preparation	\$ -775	\$ -	\$ -775		
Mucuri	0	Plantation	\$ -928	\$ -	\$ -928		
Mucuri	0	Maintenance	\$ -232	\$ -	\$ -232		
Mucuri	1	Maintenance	\$-1,023	\$ -	\$ -922		
Mucuri	2	Maintenance	\$ -310	\$ -	\$ -251		
Mucuri	5	Logging and transport	\$ -596	\$ 2,662	\$ 1,227	\$-1,882	44.0%
Igrapiúna	0	Site preparation	\$ -775	\$ -	\$ -775		
Igrapiúna	0	Plantation	\$ -928	\$ -	\$ -928		
Igrapiúna	0	Maintenance	\$ -232	\$ -	\$ -232		
Igrapiúna	1	Maintenance	\$-1,023	\$ -	\$ -922		
Igrapiúna	2	Maintenance	\$ -310	\$ -	\$ -251		
Igrapiúna	5	Logging and transport	\$-1,106	\$ 4,945	\$ 2,278	\$ -830	75.3%