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1 **Linking plant traits to ecosystem service provision through a**  
2 **management gradient in a tropical dry forest.**

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25 **Abstract:**

26 The exploitation of pristine forests decreases their functional diversity and ecosystem service  
27 provision. The forest management strategies of some rural societies, though, can increase the  
28 provision of specific ecosystem services useful to the community. This is tightly linked to shifts  
29 in forest functional traits, but few studies have investigated the changes to multiple  
30 provisioning, cultural and regulating ecosystem services across a traditional forest  
31 management gradient. This can give insights into the role of traditional management systems  
32 in the conservation of ecosystem services. Here we used a plot network of 60 dry forest plots  
33 in Sri Lanka to test whether different forest management intensities are linked to differences

34 in forest functional traits and ecosystem service provision through different tree size classes.  
35 Furthermore, we investigated the link between functional traits and ecosystem service  
36 provision with both redundancy analysis and linear mixed models. We found that the most  
37 intensely managed forest plots had some early successional traits such as light wood, small  
38 seeds and large leaves but, unexpectedly, taller trees than the least intensely managed plots.  
39 The intensely and moderately managed plots had a greater abundance of species delivering  
40 cultural and provisioning services than the least managed plots. We found significant links  
41 between the provision of construction services and mean tree height, and the delivery of  
42 cultural services and wood density. The links between functional traits and ecosystem  
43 services were clearest for individuals smaller than 10 cm DBH. Overall, the forest use and  
44 management by this rural community increased ecosystem provisioning services. For the first  
45 time we have characterised different links between species' functional traits and the  
46 ecosystem services they provide in a tropical dry forest. We highlight that the differences  
47 across forest management intensities were clearest for trees in the smaller cohorts, which  
48 are generally ignored by many studies. Similar studies will identify relevant functional traits  
49 that will help discover new species providing key ecosystem services. Understanding the  
50 interactions between rural societies and the forests they manage will foster the creation of  
51 guidelines for sustainably enhancing forest cultural and provisioning services.

52 **Keywords:** agroforestry; forest disturbance; functional diversity; provisioning services; Sri  
53 Lanka; traditional forest management.

54

## 55 1 Introduction:

56 Forests provide crucial ecosystem services particularly to rural and traditional societies (Díaz  
57 et al. 2006). Humans, however, modify vegetation structure (Maezumi et al. 2018) and tree  
58 species composition (Ross 2011; Jones et al. 2016; Levis et al. 2018; Odonne et al. 2019) of  
59 the forests they use. The changes to forest structure and composition often result in a shift in  
60 forest functioning due to an alteration to the forests' functional trait composition (Berenguer  
61 et al. 2018). For example, carbon storage can decrease after a post-exploitation alteration in  
62 forests' maximum height (Finegan et al. 2014) or after a post-disturbance decrease in mean  
63 wood density (Berenguer et al. 2018).

64 Generally, the exploitation of pristine forests results in a decrease in functional traits' diversity  
65 and this drives a decline in ecosystem service delivery (Brown et al. 2013; Cadotte et al. 2011;  
66 Eguiguren et al. 2019). This happens because the delivery of forests' ecosystem services is  
67 tightly linked to forest functional diversity (Tilman et al. 1997; De Bello et al. 2010).  
68 Nonetheless, some forms of forest management such as forest gardens and agroforestry can  
69 increase the provision of specific ecosystem services useful to the local population (such as  
70 medicine, food and construction material among others) when compared to non-managed or  
71 native forests (Armstrong et al. 2021; Wiersum 2004). Examples of forest gardens are the  
72 "Simpukng" system adopted by the Dayaks of Borneo, who increase the abundance of trees  
73 bearing non-timber forest products in secondary forest (Mulyoutami et al. 2009), or the  
74 "Ifugao woodlots" where the Ifugao people of Philippines enrich swidden fallows with  
75 construction and medicinal tree species (Rondolo 2000). A more extensive forest  
76 management system is the process defined as "landscape domestication" (Levis et al. 2018)  
77 adopted by Amazonian indigenous people. This resulted in a pan-Amazonian distribution of

78 useful species, such as *Euterpe oleracea*, a palm with edible fruits, or the Brazil nut tree  
79 *Bertholletia excelsa* (Clement et al. 2015).

80 When undertaking such management, local populations might favour species with, e.g. fleshy  
81 fruits and large seeds, functional traits indicating tree species with vertebrate dispersal  
82 (Thomson et al. 2010) and thus possibly edible for humans too (Odonne et al. 2019). Also,  
83 species with dense wood might be appreciated, such as *Eusideroxylon zwageri* (Mulyoutami  
84 et al. 2009), because high values of this functional trait indicates resistance and endurance to  
85 decay (Irawan et al. 2015). Depending on the management practices adopted (e.g. removing  
86 non-useful plants, or protection and planting of useful plants; Levis et al. 2018), the shift in  
87 functional traits may be more prevalent in certain tree size classes. For example, if the local  
88 population propagate a useful large-leaved species, we would expect to find an initial high  
89 abundance of such species and thus an increase in mean leaf size among the smallest size  
90 classes when the planting has been recent. Whereas, if the population exploits only the large  
91 individuals of a useful heavy-wooded species, we expect to see a decrease in overall wood  
92 density among trees of the largest size classes. Moreover, only few studies have included  
93 understory trees while assessing changes in ecosystem services and functional traits after  
94 land management (Mandle and Ticktin, 2015), although the understory is fundamental to  
95 understand successional trajectories (e.g. Döbert et al. 2017). It is thus of interest to study  
96 how forest use by local populations influences a forest's functional composition, functional  
97 diversity and ecosystem service provision, and ecosystem service provision through different  
98 tree sizes.

99 Ecosystem services are categorized as provisioning services, supporting services, regulating  
100 services and cultural services (Millennium Ecosystem Assessment 2005). Whilst a good body

101 of literature has investigated how singular groups of ecosystem services change after a forest  
102 is exploited (e.g. Berenguer et al. 2018; Finegan et al. 2014; Poorter et al. 2021) few studies  
103 have investigated how forest management might simultaneously affect multiple ecosystem  
104 services, rather than one group alone. Furthermore, despite the fundamental role that  
105 functional traits play in regulating the delivery of provisioning ecosystem services, there is a  
106 paucity of studies linking functional traits to provisioning ecosystem services (but see Cámara-  
107 Leret et al. 2017 for palms and Hanisch et al. 2020 for grasslands). Such links could help the  
108 search for a range of possible candidate species that might deliver a particular provisioning  
109 service (Coley et al. 2003) by e.g. research developing new agroforestry systems. This can be  
110 a useful approach especially in the tropics, where the traditional forest dwellers might have  
111 overlooked useful, but rare and thus difficult to obtain, species. In Bolivian dry forests, for  
112 example, rare species or species located in sites difficult to access are perceived as less useful  
113 (Thomas et al. 2009). Nonetheless, rare species related to useful common species would not  
114 replace the useful and common species in their usage, but they could, for example, provide  
115 new molecules with slightly different medicinal use, or genetic material to improve cultivated  
116 species (Coley et al. 2003; Souza et al. 2018).

117 Tropical dry forests are scattered across all the tropics (Miles et al. 2006) and have undergone  
118 some of the most extensive conversion to agricultural land (Hoekstra et al. 2005) due to high  
119 population densities (Bush et al. 2015). The remaining tropical dry forests are still central to  
120 human livelihoods and are of highest priority for conservation action (Miles et al. 2006). In Sri  
121 Lanka tropical dry forests cover the majority of the northern and eastern part of the island.  
122 These forests host over 200 tree species, 70 % of which are endemic to, and sustain, the Sri  
123 Lankan biodiversity hotspot (Gunawardene et al. 2007). Tropical dry forests of northern Sri  
124 Lanka are largely derived from the regeneration of forests degraded some centuries ago and

125 are inhabited by a rural society that manages such forests through shifting cultivation to  
126 different extents (Perera 2001). To date, though, it is unknown how these rural societies'  
127 management practices affect forest functional trait composition and ecosystem service  
128 provision.

129 Due to the increasing pressure of the world's population on the remaining tropical dry forests  
130 (Miles et al. 2006), our overarching aim is to understand the impact of traditional forest  
131 management practices on tropical dry forests' traits and ecosystem service provision. In this  
132 study we aim to: 1) understand how forest use by local communities affects the forests'  
133 functional trait composition across size classes, and its functional diversity, 2) characterise  
134 ecosystem service provision by tropical dry forests under different management intensities  
135 and through different size classes, and 3) characterise the links between ecosystem service  
136 delivery and functional traits.

## 137 **2 Method:**

### 138 **2.1 Study site:**

139 This study took place in the Man and Biosphere (MAB) Hurulu Forest Reserve, in northern-  
140 central Sri Lanka (8°13'N, 80°51'E; Figure 1). Man and Biosphere reserves are used to  
141 understand how traditional human activity can be reconciled with nature conservation (Reed  
142 2019). The reserve hosts dry tropical forest, a forest type that covers 47,753 km<sup>2</sup> in Sri Lanka  
143 with 37 % of this area under formal protection (Dinerstein et al. 2017). The Hurulu reserve  
144 receives a mean annual precipitation of c. 1400 mm and undergoes a dry period of three  
145 months (< 50 mm monthly precipitation) from May to August (Medawatte et al. 2021). The

146 forest reserve is inhabited by villagers that practice shifting cultivation system called Chena,  
147 mainly cultivating rice and living off forest-gardens. The number of dwellers is unknown.

## 148 **2.2 Management intensity assessment:**

149 We classified the Hurulu Forest Reserve according to a “management intensity”  
150 categorization to account for the extent to which the forest is used by locals (Medawatte et  
151 al. 2021). To this end, we subdivided the forest area into 400 grid cells of 1 km x 1 km with an  
152 image resolution of at least 15 m (Supplementary information Figure 1; Images are sourced  
153 from Google Earth). For each cell we calculated a management intensity score by assessing  
154 the presence (1) or absence (0) of nine management factors which were: a) road or jeep tracks,  
155 b) shifting cultivation areas, c) forest plantations, d) partially logged areas, e) permanent non-  
156 paddy agricultural lands, f) human settlements, g) grasslands, h) paddy fields, and i) other  
157 signs of management. The presence of these factors were ground- truthed with field surveys.  
158 This allowed us to group the forest reserve into three management intensity clusters, which  
159 are least management intensity (score of 0-1), moderate management intensity (score of 2-  
160 3) and high management intensity score  $\geq 4$ ) (Medawatte et al. 2021). We choose to use three  
161 management intensity categories because it allows us to better describe the sites rather than  
162 a disturbed – not disturbed classification, while minimizing the number of classes.

## 163 **2.3 Floristics, functional traits and ecosystem services:**

164 In each of the three management intensities we randomly installed 20 plots of 10 m x 20 m.  
165 In each plot, we measured the diameter at breast height (DBH; 130 cm) and identified all living  
166 woody plants  $\geq 1$  cm DBH to species level (only 1.3 % of stems were not identifiable so were  
167 segregated to morphospecies, leading at total of 108 taxa).



168 We considered four functional traits with established links to ecosystem functions, spanning  
169 a) competitive ability traits such as maximum tree height, b) dispersal and colonisation  
170 potential traits, such as seed mass, c) stress tolerance traits, such as wood density, and d)  
171 resource acquisition traits such as leaf length. We obtained maximum tree height from Ashton  
172 et al. (1997). We measured leaf length from the illustrations of Ashton et al. (1997) using the  
173 ImageJ software (Schneider et al. 2012). If a species was not available or it did not have a  
174 reference scale in Ashton et al. (1997), we used the herbarium images of several individuals  
175 from each species, obtained from the Royal Botanic Garden Plants of the World Online  
176 database (<http://powo.science.kew.org/>). By choosing the leaf measures of Ashton et al.  
177 (1997) we did not account for the variability of this functional trait within each species, and  
178 the measure is likely biased by the author of the drawings. Nonetheless this method is valid  
179 because Ashton et al.'s (1997) drawings represent average species' leaf lengths of plants  
180 grown in Sri Lanka. We obtained tree wood density from the Global Wood Density Database  
181 (Zanne et al. 2009). When the wood density of the target species were not available, we  
182 averaged the available data for congeneric species from the same geographic area, as  
183 suggested by Flores and Coomes (2010) and Jucker et al. (2016). We obtained seed weight  
184 from the Royal Botanic Gardens Kew Seed Information Database (SID, 2020). When data for  
185 species were missing from the relevant database, we used genus mean, a family mean or a  
186 basal area-weighted mean value across all plots (Supplementary Table S1). We adopted the  
187 same protocol for unidentified species. This was done in order to avoid biasing the mean value  
188 with missing data.

189 To characterise forest ecosystem service delivery, we first defined five types of services: 1)  
190 construction, which consisted of species used for building; 2) cultural, which consisted of  
191 species used to create batik, dyes, perfumes, cosmetics, temple offerings, ornamental or

192 sacred species; 3) food, which consisted of edible species; 4) household, which consisted of  
193 species used to make soap, utensils, insecticide, lacquer, charcoal, rope etc., and 5) medicinal,  
194 which consisted of medicinal species. We assigned all species a value of 1 or 0 if the specific  
195 species was (1) or was not (0) used for construction, cultural, food, household or medicinal  
196 services. We obtained this information from Ashton et al. (1997). We then calculated the  
197 abundance of each identified species per plot and multiplied the abundance by 1 or 0 in the  
198 case that a species provided, or did not provide, a specific ecosystem service. We then  
199 summed the value for each service in every plot. Assigning species a value of 1 or 0 in case  
200 they provide, or not, a service is a very simplistic technique and we assume that 1) species  
201 abundance is proportional to the quantity of ecosystem service that each species provides  
202 and 2) species that provide the same ecosystem service have the same coefficient of  
203 proportionality. This is an adequate simplification given that we perform the analysis on  
204 separate size classes, thus limiting tree size variation within a plot. We study the potential of  
205 species to furnish their service (e.g. we account a species as “food species” even if the  
206 individuals are too immature to provide food) and we had no information on the differences  
207 of coefficient proportionality across species. We based the analysis on stem count and not on  
208 basal area because our study plots are small, and having e.g. one big tree in a plot could bias  
209 the ecosystem service delivery of the plot, overlooking other important or interesting species  
210 with smaller individuals within the same size class. We performed these analyses sub-setting  
211 the trees into four size categories: i)  $< 5$  cm DBH, ii)  $\geq 5$  cm DBH and  $< 10$  cm DBH, iii)  $\geq 10$  cm  
212 DBH and  $< 20$  cm DBH, and iv)  $\geq 20$  cm DBH.

213

## 214 **2.4 Statistical analysis:**

### 215 **2.4.1 Differences in functional traits between management intensity:**

216 In this study we adopt the functional diversity approach of Villéger et al. (2008) that split  
217 functional diversity in three indices. These were functional richness (the amount of  
218 multivariate niche space filled by species in the community), functional evenness (evenness  
219 of the distribution of abundance in occupied niche space) and functional divergence (degree  
220 to which abundance distribution in niche space maximizes the total community variation in  
221 functional characters) (Laliberté & Legendre 2010; Villéger et al. 2008). We also calculated  
222 functional dispersion (mean distance of all species from the centroid of all species in the  
223 community) (Laliberté and Legendre, 2010). Functional traits were standardized before  
224 calculating the functional diversity metrics. We adopted the approach of Villéger et al. (2008)  
225 because these indices take into consideration multiple traits, are independent of species  
226 richness and consider species abundance. This is important because we studied a species-rich  
227 landscape that contains rare species. If using an index independent of species abundance, like  
228 the dendrogram based functional diversity index of Petchey and Gaston (2007), rare species  
229 could bias the index, increasing functional diversity although the species is present only as a  
230 single individual.

231 We studied the impact of human use of forest on functional trait composition by calculating  
232 and comparing the relative abundance-based community weighted mean (CWM) values of  
233 leaf length, maximum tree height, wood density and seed weight using a one-way ANOVA on  
234 plots' mean values followed by a Tukey's HSD test.

### 235 **2.4.2 Differences of ecosystem services provision among management intensity:**

236 To characterise forests' ecosystem services provision among different management  
237 intensities we used Principal Component Analysis (PCA) on the centered and scaled relative

238 abundance of species delivering specific ecosystem services (see 2.3). We used one plot-by-  
239 ecosystem service matrix for each of the four size classes. We tested the significance of forest  
240 management intensity (i.e. least, moderate and high) with a multivariate permutational  
241 analysis of variance using Bray-Curtis distance matrix (r function *adonis* with 999  
242 permutations).

### 243 **2.4.3 Relationship between species' provisioning services and species' functional traits:**

244 We inspected whether the variation in species' provisioning services could be explained by  
245 the species' functional traits with a redundancy analysis (RDA; significance assessed by 999  
246 permutations). For this analysis, we constrained the ecosystem services with functional traits  
247 at species' level. We then tested whether the associations between ecosystem service  
248 provision and functional traits found by the RDA at species level scaled to the plot level. We  
249 tested this with linear mixed model (LMM) selection based on the lowest Akaike Information  
250 Criteria (AIC). In the LMM, the response variables were plots' abundance-weighted-mean  
251 ecosystem services delivery, the fixed effect were the scaled and centred plot abundance-  
252 weighted mean functional traits, and the random effects were plots' management intensity.  
253 In total, we built 15 models (Supplementary Table S2). We calculated models' marginal  $R^2$   
254 (describing the variance explained by the fixed effects alone) and conditional  $R^2$  (describing  
255 the variance explained by the whole model) to assess models' goodness of fit (Nakagawa and  
256 Schielzeth, 2013). We derived the significance for the singular fixed effects' variables using t-  
257 tests with Satterthwaite's approximation to estimate degrees of freedom on the best model  
258 for each ecosystem service. We checked the models for normality of the residuals by  
259 inspecting standard quantile-quantile plots.

260 We calculated the abundance-based functional traits CWM and functional indices with the FD  
261 R package (Laliberté et al. 2014), the Tukey's HSD test with the agricolae R package (de

262 Mendiburu 2020), the PCA with the factoextra R package (Kassambara and Mundt, 2020), the  
263 RDA with the vegan R package (Oksanen et al. 2019), the LMM with the lme4 package (Bates  
264 et al. 2020), calculated t-tests' p-values for the singular fixed effect with the lmerTest package  
265 (Kuznetsova et al. 2019) and LMM's  $R^2$  with the performance package (Lüdecke et al. 2020) in  
266 R 3.5.1 (R Development Core Team 2009).

267

### 268 **3 Results:**

269 Functional divergence was greatest in moderately managed forests ( $p < 0.05$ , Table 1) and  
270 functional dispersion was greater in the least managed forest compared to the most intensely  
271 managed forest ( $p < 0.05$ ) but not the moderately managed forest.

272 The ANOVA and Tukey test showed that mean leaf length was longer in moderately managed  
273 forest when compared to highly managed forests and forests with the least management  
274 intensity, and wood density was significantly greater in the least managed plots – both of  
275 these patterns were seen in the two mid-size categories (i.e. 5-10 cm DBH and 10-20 cm DBH),  
276 although there was only a non-significant trend for the leaf length of the least managed forest  
277 in the 5-10 cm DBH size class and the wood density of the moderate intensity managed forest  
278 in the 10-20 cm DBH size class. The mean seed weight was significantly heavier in the least  
279 managed plots throughout the 1-5 cm, 5-10 cm and 10-20 cm size classes. The mean species'  
280 maximum height was shortest in the least managed plots for trees size categories up to 20  
281 cm DBH (Figure 2).

282 The adonis test showed that delivery of the ecosystem services was significantly different  
283 among forest management intensities for trees smaller than 20 cm DBH, represented in the

284 PCAs of Figure 3. When considering trees in the two smallest size classes (1-5 and 5-10 cm  
285 DBH) the PCA showed highly managed forests to have a greater abundance of trees providing  
286 food, medicinal and cultural resources in comparison to plots with least management  
287 intensity, and moderately managed plots to have greater abundance of individuals providing  
288 household resources or used for construction in comparison to the least managed forest plots  
289 (Figures 3 a & b). A similar pattern was seen for trees 10-20 cm DBH but, for this size class,  
290 moderately managed and the least managed forest plots were similar to one another (Figure  
291 3 c). When considering only trees > 20 cm DBH, there was no significant differences in  
292 ecosystem service delivery among different management intensities (Figure 3 d).

293 The RDA first axis (Figure 4) explained 69 % of the constrained variance and was characterised  
294 by species with or without construction value ( $p < 0.001$ ), which was best explained by  
295 differences in maximum tree height ( $p < 0.001$ ). The second RDA axis explained 20 % of the  
296 constrained variance and was characterised by species with food ( $p < 0.001$ ) and cultural value  
297 ( $p < 0.001$ ) as well as species with household value ( $p < 0.05$ ), and this was best explained by  
298 species' wood density ( $p < 0.01$ ).

299 The results of LMM were similar to the RDA results. The construction service value of a plot  
300 was greater if there were either more tall species or more individuals of a tall species in the  
301 plot ( $p < 0.001$ ; Table 2). Another model agreeing with the RDA results found that plots with  
302 high cultural service provision had species with dense wood ( $p < 0.001$ ) and a taller stature ( $p$   
303  $< 0.01$ ). The provision of food, on the other hand, was greater in plots with shorter trees ( $p$   
304  $< 0.01$ ) and heavier seeds ( $p < 0.05$ ), household service provision was greater in plots with  
305 lighter seeds ( $p < 0.001$ ) and larger leaves ( $p < 0.01$ ), and medicinal provision was more

306 abundant in plots having tall species ( $p < 0.001$ ) with long leaves ( $p < 0.001$ ) and dense wood  
307 ( $p < 0.05$ ).

308

## 309 **4 Discussion:**

310 Management of forests by local populations usually drives a shift in tree species composition  
311 with consequent changes in functional diversity and ecosystem services delivery, though most  
312 studies focus on species composition alone or singular groups of ecosystem services (e.g.  
313 Berenguer et al. 2018; Armstrong et al. 2021). Here we assessed dry tropical forest functional  
314 composition differences across a gradient of human management-driven disturbance, linking  
315 differences in trait composition to the delivery of multiple provisioning and cultural  
316 ecosystem services. We acknowledge that, in further studies, it would be useful to do a  
317 sensitivity analysis on the number of management intensity classes.

### 318 **4.1 Functional diversity:**

319 Here we show that functional dispersion decreased through the management gradient and  
320 that functional divergence was greater in moderately managed forest plots. Functional  
321 dispersion (which is often used as a proxy for functional diversity) has been shown to bear  
322 both positive (Carreño-Rocabado et al. 2012; Döbert et al. 2017) and negative (Flynn et al.  
323 2009; Ziter et al. 2013) correlations with disturbance. This duality is probably linked to the  
324 type of disturbance and to the selective pressure present in the “undisturbed” environment  
325 (Döbert et al. 2017). For instance, a closed canopy forest would increase in functional  
326 dispersion when a broader light gradient is introduced by disturbance. In our case, we

327 speculate that the management of forests reduced the micro-variability of the light  
328 environment, thus decreasing functional dispersion.

329 High functional divergence indicates a selection for opposing functional traits, highlighting a  
330 coexistence of several life strategies due to spatial heterogeneity (Mason et al. 2005; Raavel  
331 et al. 2012). The moderately managed forests thus might attain high functional divergence  
332 because they might have been populated by species typical of both the most managed and  
333 the least managed habitats, which have divergent sets of traits, bearing similarities to the  
334 intermediate disturbance hypothesis (Connell 1978). This result agrees with studies assessing  
335 high functional diversity in a forest previously managed by indigenous people in the Pacific  
336 North West of Canada (Armstrong et al. 2021).

337 The community weighted mean of plant functional traits were significantly different between  
338 management intensities although the patterns (and their statistical significance) changed  
339 among tree size classes. Our results are in accordance with studies showing that human  
340 disturbance to forested sites favour species with light wood and small seeds (Hawes et al.  
341 2020; Carreño-Rocabado et al. 2012). Seed size, for example is related to tree species'  
342 dispersal mode, and a shift to smaller seeds indicates fewer vertebrate-dispersed tree species  
343 (Thomson et al. 2010). Such changes could be ascribed to a shift toward a more "acquisitive"  
344 composition of managed forests in contrast to non-managed forests, and could be regarded  
345 as a step of forest succession. Acquisitive species are characterised by shade intolerance,  
346 shorter stature, faster growth rates and less dense wood whereas conservative species are  
347 usually shade tolerant, taller, with slower growth rates and denser wood (Díaz et al. 2004;  
348 Mankou et al. 2021; Reich 2014). Along a successional gradient, undisturbed forests have a  
349 more "conservative" set of traits and disturbed forests have a more "acquisitive" set of traits



350 (Swaine and Whitmore, 1988; Slik et al. 2008; Chazdon et al. 2010; Both et al. 2018).  
351 Nonetheless, under the framework of a shift to an “acquisitive” forest composition, the  
352 finding of taller trees in the most intensively managed forests is unexpected. Even if it is true  
353 that plant height is influenced by a multitude of factors, secondary forests (rich in “acquisitive”  
354 species) are generally shorter than primary forest (rich in “conservative” species) (Richards  
355 1973, [Peña-Claros](#) 2006). This suggests that the difference among the three management  
356 intensities may be driven not by succession but by human management that favoured a  
357 particular set of tall statured species which have also a secondary use beside construction,  
358 thus making these species more useful to the population, such as *Albizia odoratissima*  
359 (Fabaceae; medicinal value), *Lannea coromandelica* (Anacardiaceae; food, medicinal and  
360 household value), *Cinnamomum cassia* (Lauraceae; food and medicine value) and *Tamarindus*  
361 *indica* (Fabaceae; food, medicinal, cultural and household value) which were present only in  
362 the intensely managed plots. We thus argue that the differences of functional traits between  
363 management intensities are driven by active human management rather than natural forest  
364 succession and favour species with multiple uses.

365 Differential responses of functional traits among size classes has also been observed in South  
366 African coastal forest. In this case seedlings showed less significant changes in community  
367 weighted mean traits across habitats than adult trees (Rolo et al. 2016). We believe that the  
368 differential responses of functional traits among management intensities across size classes  
369 highlights that shifts in functional traits are driven by different processes in this forest. For  
370 instance, the difference in seed weight and maximum tree height was significant for the  
371 smallest cohort (trees < 5 cm DBH) and we speculate that this pattern is driven by a  
372 differential recruitment of seedlings, possibly due to planting/sowing of useful species by the  
373 local population (A. Medawatte, personal observation). On the other hand, where differences

374 in functional traits are significant only for medium-sized trees (trees  $\geq 5$  cm DBH and  $< 20$  cm  
375 DBH), such as for wood density and leaf length, we speculate that the driver of change in  
376 functional traits is due to a harvest strategy aimed at a specific tree size. In Benin, for example,  
377 over-harvesting of the large individuals of *Khaya senegalensis* decrease, obviously, the density  
378 of large individuals, but also the density of seedlings of this species, leaving a large number of  
379 medium-size trees (Gaoue and Ticktin, 2007). If the harvested species has e.g. dense wood,  
380 the mean wood density will increase only for the medium size-classes.

#### 381 **4.2 Ecosystem services:**

382 The difference in ecosystem services provision was highly significant across management  
383 intensities for trees  $< 10$  cm DBH, significant for trees  $\geq 10$  cm DBH and  $< 20$  cm DBH, but not  
384 significant when considering trees  $> 20$  cm DBH (Figure 3). These differences could be  
385 explained by a differential size preference for different services (e.g. there could be a cultural  
386 use that mainly requires trees of 5-20 cm DBH). Our results, nonetheless, show that in the  
387 moderately and highly managed forests there are many tree species that deliver provisioning  
388 services, in particular construction and household services for moderately managed forests,  
389 and medicine as well as food for highly managed forests. This supports the idea that local  
390 populations introduced or favoured the growth of livelihood-supporting tree species. Under  
391 this framework, the RDA analysis, at species level, and the LMM, at plot level, showed a  
392 significant link between construction value (most abundant in moderately managed forests)  
393 and maximum height (significantly taller in managed forests). This allows us to speculate that  
394 the local population favoured the presence of tall species to use their wood when trees  
395 mature. The link between medicinal usage, tree height and wood density was visible only at  
396 at plot level (LMM) and not at species level (RDA). So, plots with high medicinal value have  
397 many tall species, but these are not necessarily medicinal species. We speculate that tall

398 species could be used to shade small, fast growing medicinal plants. The framework proposed  
399 by Coley et al. (2003) that acquisitive species invest in rapid tree growth (which does not  
400 entails taller trees, but just quicker growth) and N-based chemical defence by producing  
401 alkaloids, a particular group of medicinally interesting compounds. The link between the  
402 provision of food, short tree stature, which favours fruit collection, and large seed size, which  
403 indicate vertebrate dispersal, could indicate a domestication syndrome (Milla et al. 2015) at  
404 the plot level, where the population has been favouring edible fruit-bearing plant species. The  
405 relationship between wood density and cultural services is less intuitive but we speculate that  
406 perhaps longer-lived trees (which usually have denser wood e.g., Chao et al. 2008) have a  
407 longer period of time to develop cultural 'value'. Of the 11 plant species with a cultural value,  
408 seven had a wood denser than the average species' wood density, and none of these had  
409 more than 34 individuals throughout the dataset. So this trend is unlikely to be driven by one  
410 very abundant species. An example of species with high wood density and cultural value is  
411 *Tamarindus indica*, which is present only in highly managed forests. Another species, this time  
412 present only in non-managed forest, is *Mesua ferrea* (Calophyllaceae), a native Sri Lankan tree  
413 known locally as Sri Lankan Ironwood and raised to the status of Sri Lanka's national tree. The  
414 plant species' services we inferred from Ashton et al. (1997) are traditional uses of the plants,  
415 which could have changed through the last decades due to the introduction of modern  
416 solutions such as plastic for utensils or synthetic products for cosmetics and insecticides.

417

## 418 5 Conclusion:

419 In this work we studied the effect of local communities' forest management on forest  
420 functional traits and forest ecosystem services provision throughout increasing tree size  
421 classes and, as a novel contribution, we assessed the links between them. The difference in  
422 tree functional traits along a management gradient was most clear for trees between 5 cm  
423 and 20 cm DBH, with the least managed plots having trees with denser wood, heavier seeds  
424 and, somewhat surprisingly, lower stature. Managed plots had a greater abundance of trees  
425 delivering provisioning services to the local population, in accordance with the literature on  
426 agroforestry and forest gardens. These services were related to the presence of taller trees  
427 (construction and medicinal services) or with denser wood (medicinal and cultural services).  
428 We suggest that this is the effect of selective practices of the local population, which might  
429 have favoured useful species. We highlight that, in our plots, the differences in ecosystem  
430 service provision across the management intensity gradient were most clear for trees  
431 between 1 cm and 10 cm DBH. Although we do not deny the undisputed importance of  
432 unmanaged natural forests for the provision of crucial regulating ecosystem services (Watson  
433 et al. 2018), we believe that knowledge on the interaction between local societies and  
434 ecosystems is important to safeguard such forests without excluding their dwellers, an  
435 increasingly recognised necessity (Vermeulen and Sheil 2007; Fa et al. 2020). Furthermore,  
436 acknowledging managed forests' provision of ecosystem services might help to justify the  
437 protection of these forests and their dwellers, preventing land conversion to less performing  
438 land uses, as it is occurring throughout the tropics. Preserving these managed forests and the  
439 practices of the local communities will allow, and possibly foster, forest restoration  
440 endeavours, in the future.

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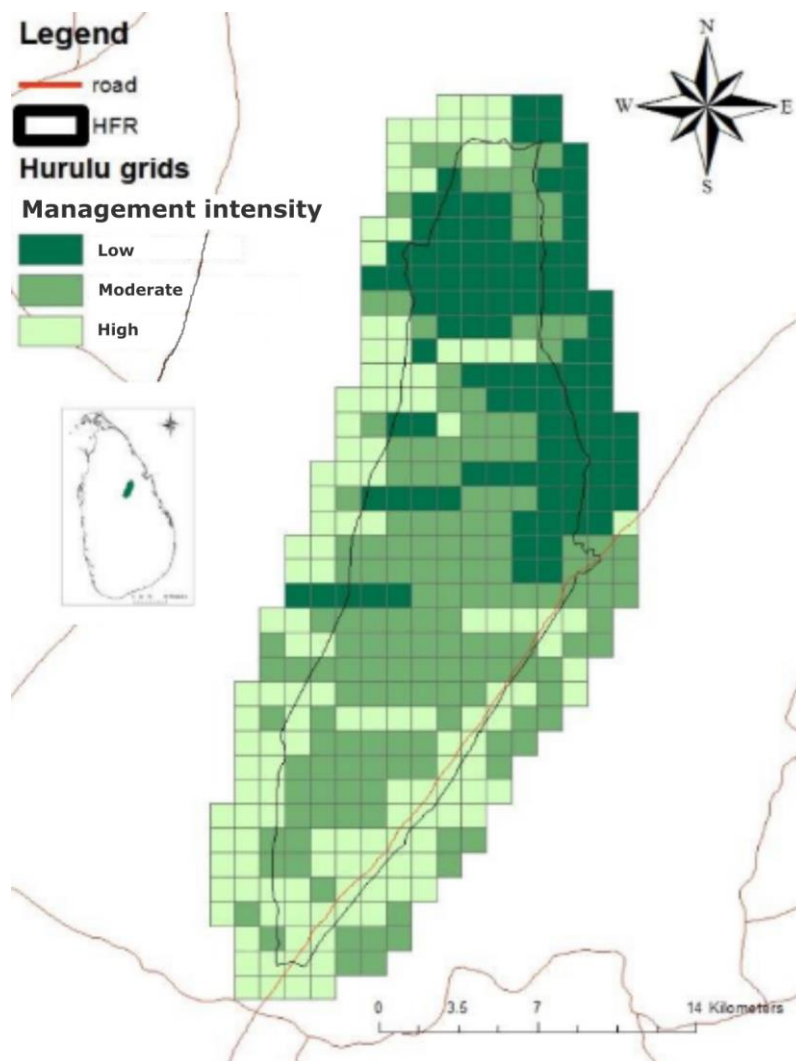
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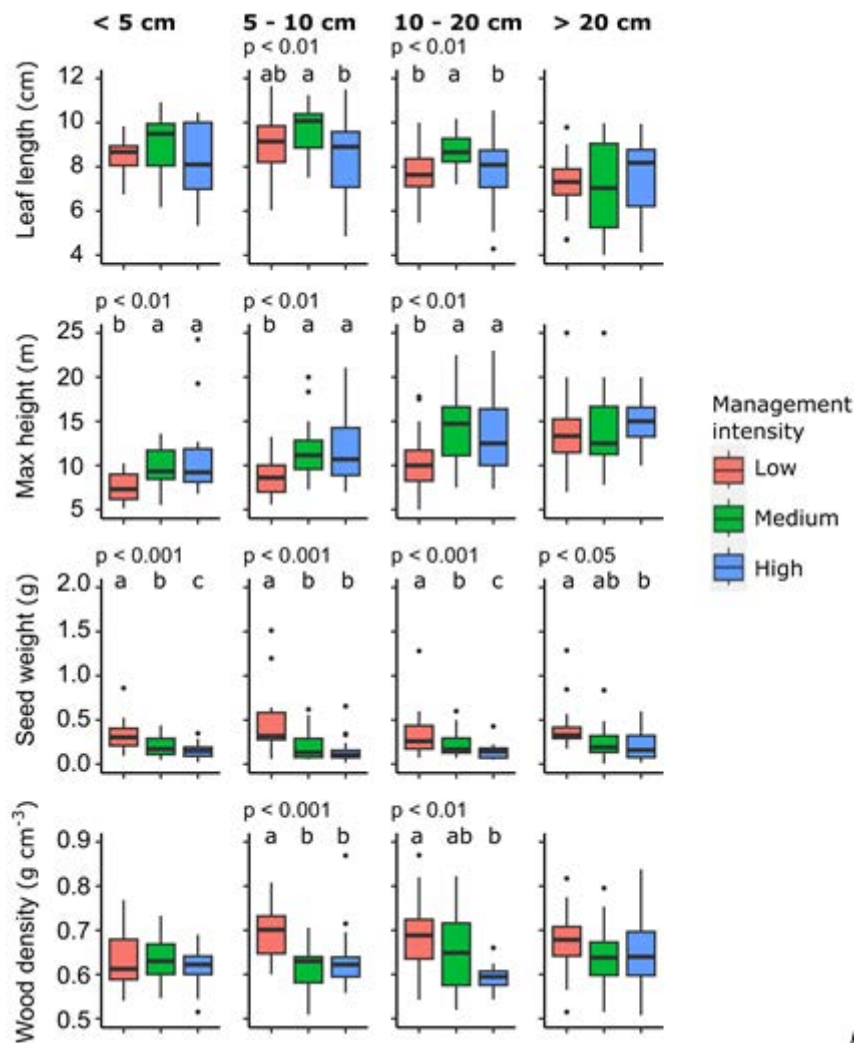
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694 8 Figures and tables



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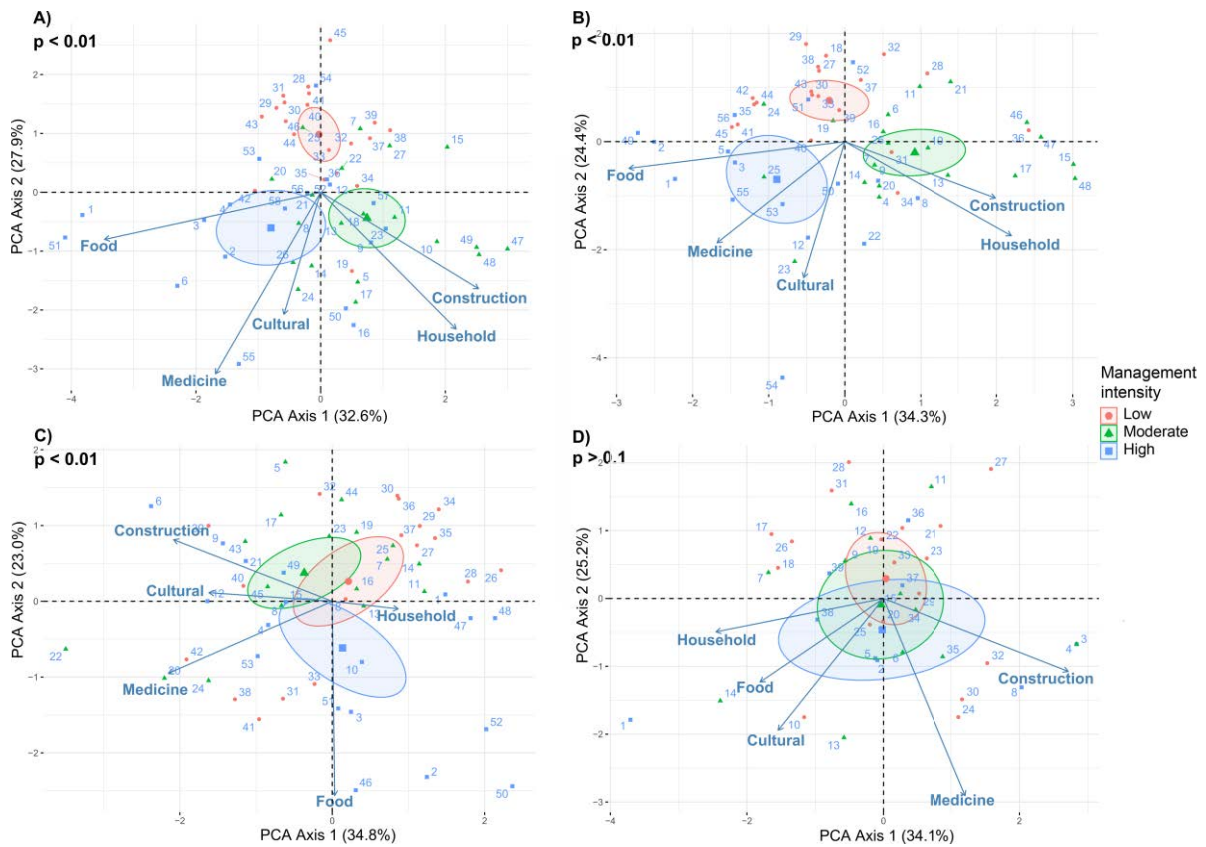
696 *Figure 1. Location of the Hurulu Forest Man and Biosphere Reserve, a dry tropical forest in*  
697 *Sri Lanka. Figure modified from Medawatte et al. (2021)*



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700 *Figure 2 Differences in community weighted mean functional traits across a forest*  
 701 *management intensity gradient in the dry tropical forest of the Hurulu Forest Reserve, Sri*  
 702 *Lanka. The significance values are calculated with one-way ANOVA and Tukey HSD tests. The*  
 703 *four columns (from left to right) represent the results for the analysis for trees < 5 cm DBH,*  
 704 *trees ≥5 cm DBH and < 10 cm DBH, trees ≥ 10 cm DBH and < 20 cm DBH and trees ≥ 20 cm*  
 705 *DBH.*

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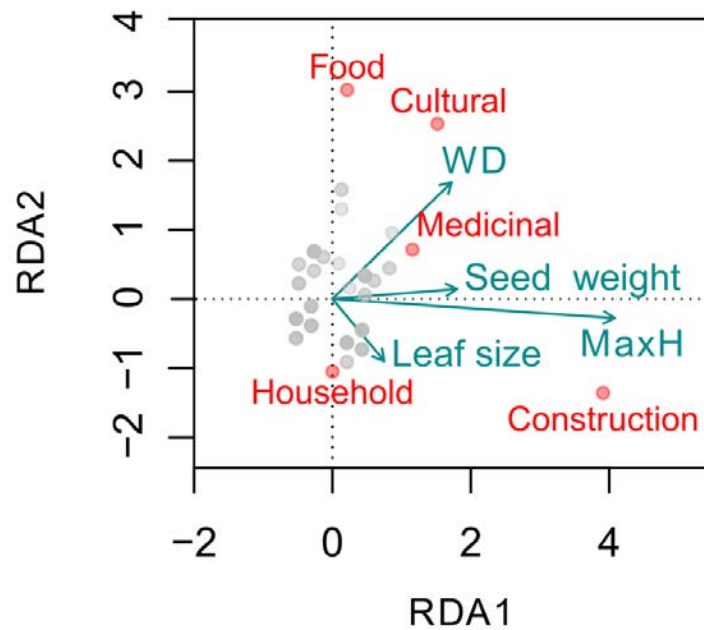
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708 *Figure 3 Principal Component Analysis of plots' ecosystem services provision across a*  
709 *management intensity gradient in the dry tropical forest of the Hurulu Forest Reserve, Sri*  
710 *Lanka. We performed the analysis separately for A) trees < 5 cm DBH, B) trees  $\geq 5$  cm DBH and*  
711 *< 10 cm DBH, C) trees  $\geq 10$  cm DBH and < 20 cm DBH and D) trees  $\geq 20$  cm DBH. The forest*  
712 *plots are indicated with numbers, the ellipses represent the 95 % confidence interval around*  
713 *the management intensity centroid and the p-value is obtained by a multivariate*  
714 *permutational ANOVA on a distance matrix (adonis function).*

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719 *Figure 4 Redundancy analysis (RDA) biplot with species' ecosystem service provision (red)*  
 720 *constrained by species' selected functional traits (blue) in the dry tropical forest of the Hurulu*  
 721 *Forest Reserve, Sri Lanka. The grey points are the species and their positions represent the*  
 722 *possible combinations of ecosystem services provision that each species can have. Given the*  
 723 *binary character of ecosystem services, species' position is limited to a maximum of 32*  
 724 *positions, so species' grey intensity is weighted by the number of species occurring on that*  
 725 *point.*

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728 *Table 1 Mean value (±SE) of four functional diversity indices across three management*  
 729 *intensities in the dry tropical forest of Hurulu Forest Reserve, Sri Lanka. We tested variables*  
 730 *significance across the management intensities with ANOVA and Tukey's HSD tests.*

Management intensity	Functional richness	Functional evenness	Functional divergence	Functional dispersion
Low	4.33(±0.48)	0.69(±0.02)	0.73(±0.02) <sup>b</sup>	1.61(±0.08) <sup>a</sup>
Moderate	3.89(±0.52)	0.71(±0.02)	0.81(±0.02) <sup>a</sup>	1.52(±0.04) <sup>ab</sup>
High	3.45(±0.78)	0.69(±0.02)	0.73(±0.03) <sup>b</sup>	1.34(±0.08) <sup>b</sup>
p-value	> 0.05	> 0.05	< 0.01	< 0.05

Table 2 Summary statistics of the best linear mixed models (selected by the lowest AIC, see Table S3) to understand links among plots' ecosystem services delivery and the centred and scaled functional traits in the dry tropical forest of the Hurulu Forest Reserve, Sri Lanka.  $R^2_C$  and  $R^2_M$  stand for conditional and marginal  $R^2$ , respectively. Functional traits' significance was calculated by t-tests with Satterthwaite's approximation to estimate the degrees of freedom. Significance symbols are as follows: '\*\*\*' <0.001, '\*\*' <0.01, '\*' <0.05.

Ecosystem service	$R^2_C$	$R^2_M$	Plot CWM functional trait	Estimate	Std. Error	Df	t-value
Construction	0.62	0.42	Maximum height	0.13	0.02	56.72	6.82***
			Wood density	-0.02	0.01	55.99	-1.53
Household	0.33	0.31	Seed weight	-0.11	0.02	20.71	-4.01***
			Leaf size	0.07	0.02	47.40	2.77**
Food	0.56	0.13	Maximum height	-0.07	0.02	56.88	-2.91**
			Seed weight	0.05	0.02	56.99	1.96*
Medicine	0.61	0.20	Maximum height	0.08	0.02	55.05	3.73***
			Leaf size	0.07	0.02	54.75	3.42***
			Wood density	0.05	0.02	54.51	2.46*
Cultural	0.50	0.28	Wood density	0.04	0.01	55.02	5.10***
			Maximum height	0.02	0.01	55.81	2.92**
			Leaf size	0.01	0.01	55.44	1.84



732 9 Supplementary material

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736 *Table S1. Percentage of the 108 species we obtained functional traits directly from the*  
737 *literature (species), by averaging values at genus level, at family level or by calculating a basal-*  
738 *area weighted overall mean.*

	Species	Genus	Family	Overall
Leaf length	87.9	0.9	3.7	7.4
Maximum height	84.2	2.8	5.5	7.4
Seed weight	71.3	2.8	16.7	9.3
Wood density	51.8	28.7	11.1	8.3

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740 *Table S2. Structure of the 15 models used to infer links between plot mean functional traits*  
 741 *and plot mean ecosystem service provision. Abbreviations are as follows: LS = leaf size, MaxH*  
 742 *= maximum tree height, PES = provisioning ecosystem service, SW = seed weight, WD = wood*  
 743 *density. The E term included management as random effect.*

Model number	Model structure
1	$PES \sim a \text{ MaxH} + b \text{ WD} + c \text{ LS} + d \text{ SW} + E$
2	$PES \sim a \text{ MaxH} + b \text{ WD} + c \text{ LS} + E$
3	$PES \sim a \text{ MaxH} + b \text{ WD} + c \text{ SW} + E$
4	$PES \sim a \text{ MaxH} + b \text{ SW} + c \text{ LS} + E$
5	$PES \sim a \text{ WD} + b \text{ LS} + c \text{ SW} + E$
6	$PES \sim a \text{ MaxH} + b \text{ WD} + E$
7	$PES \sim a \text{ MaxH} + E$
8	$PES \sim a \text{ WD} + E$
9	$PES \sim a \text{ LS} + E$
10	$PES \sim a \text{ SW} + E$
11	$PES \sim a \text{ MaxH} + b \text{ LS} + E$
12	$PES \sim a \text{ MaxH} + b \text{ SW} + E$
13	$PES \sim a \text{ WD} + b \text{ SW} + E$
14	$PES \sim a \text{ WD} + b \text{ LS} + E$
15	$PES \sim a \text{ SW} + b \text{ LS} + E$

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