

1 Title: Potential tree species extinction, colonization and recruitment in Afromontane  
2 forest relicts

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4 Running title: Potential tree species shifts in forest relicts

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## 22 **Abstract**

23 Tree species regeneration determines future forest structure and composition, but is  
24 often severely hampered in small forest relicts. To study succession, long-term field  
25 observations or simulation models are used but data, knowledge or resources to run  
26 such models are often scarce in tropical areas. We propose and implement a species  
27 accounting equation, which include the co-occurring events extinction, colonization  
28 and recruitment and which can be solved by using data from a single inventory. We  
29 solved this species accounting equations for the 12 remaining Afromontane cloud  
30 forest relicts in Taita Hills, Kenya by comparing the tree species presence among the  
31 seedling, sapling and mature tree layer in 82 plots. A simultaneous ordination of the  
32 seedling, sapling and mature tree layer data revealed that potential species extinctions,  
33 colonizations and recruitments may induce future species shifts. On landscape level,  
34 the potential extinction debt amounted to 9% (7 species) of the regional species pool.  
35 On forest relict level, the smallest relicts harbored an important proportion of the tree  
36 species diversity in the regeneration layer. The average potential recruitment credit,  
37 defined as species only present as seedling or sapling, was 3 and 6 species for large and  
38 small forest relicts, while the average potential extinction debt was 12 and 4 species,  
39 respectively. In total, both large and small relicts are expected to lose approximately  
40 20% of their current local tree species pool. The species accounting equations provide a  
41 time and resource effective tool and give an improved understanding of the  
42 conservation status and possible future succession dynamics of forest relicts, which can  
43 be particularly useful in a context of participatory monitoring.

44

45 Key words: Community structure; forest succession; late-successional species;  
46 regeneration; restoration; secondary forest; species accounting equation; species  
47 turnover; Taita Hills

## 48 **Introduction**

49 Destruction and loss of natural habitat are major causes of biodiversity decline and  
50 species extinction (Brose 2011; Fahrig 2002; Tilman, May, Lehman & Nowak 1994).

51 Forests are one of the largest terrestrial biomes and are severely threatened by  
52 anthropogenic habitat deterioration with an estimated loss of 13 to 20 million hectares  
53 each year, of which one third is located in the tropics (FAO 2011; Hansen, Potapov,  
54 Moore, Hancher, Turubanova et al. 2013). Many plant populations strive to survive in  
55 small forest relicts (Ewers & Didham 2006) and the succession of tree species in these  
56 forest patches is a central theme in plant community ecology, restoration, and land  
57 management (Cook, Yao, Foster, Holt & Patrick 2005).

58

59 The succession within these forest relicts is driven by three major events, which can  
60 alter the species composition of forest relicts: extinction, colonization and the  
61 recruitment of seedlings and saplings to the mature tree layer. In forests, there is a time-  
62 lagged response of species to habitat modifications (Hylander & Nemomissa 2009;  
63 Jackson & Sax 2010; Metzger, Martensen, Dixo, Bernacci, Ribeiro et al. 2009),  
64 because of the long life span and regeneration time of trees (Vellend, Verheyen,  
65 Jacquemyn, Kolb, Van Calster et al. 2006). The future extinction of a species due to  
66 events that happened in the past is known as delayed extinction and quantified as  
67 extinction debt (Hylander et al. 2009; Jackson et al. 2010; Tilman et al. 1994).

68 Although only the preservation of large areas of primary forest can safeguard the  
69 complete species pool (Gibson, Lee, Koh, Brook, Gardner et al. 2011), a substantial  
70 number of forest species can survive for a long time in small and degraded forest relicts  
71 before they become extinct (Helm, Hanski & Pärtel 2006; Kuussaari, Bommarco,

72 Heikkinen, Helm, Krauss et al. 2009; Vellend et al. 2006). Especially the failure of  
73 species regeneration is a threat to future forest biodiversity and composition because  
74 species persistence depends on the availability of seeds, seedlings and saplings  
75 (Albrecht, Neuschulz & Farwig 2012; Benítez-Malvido & Martínez-Ramos 2003;  
76 Farwig, Sajita, Schaab & Böhning-Gaese 2008; Lawes, Joubert, Griffiths, Boudreau &  
77 Chapman 2007). The extinction of a species that remains present in the regional species  
78 pool (local species extinction, Fig. 1-1a), can be counterbalanced by a recolonization of  
79 this species from the regional species pool (autochthonous colonization, Fig. 1-2a).  
80 However, when a species is present in one relict only, its extinction in this patch will  
81 result in the disappearance of the species from the region (regional species extinction,  
82 Fig. 1-1b). Colonization credit is the number of species yet to colonize a forest relict  
83 (Jackson et al. 2010; Piqueray, Cristofoli, Bisteau, Palm & Mahy 2011). Such  
84 establishment of species within forest relicts is a gradual process because it depends on  
85 several external factors like landscape structure and ability of newly arrived seeds to  
86 germinate, or internal factors like succession or management (Kirika, Böhning-Gaese,  
87 Dumbo & Farwig 2010; Laurance, Nascimento, Laurance, Andrade, Fearnside et al.  
88 2006). Moreover, forest relicts are often characterized by new abiotic conditions (e.g.  
89 altered irradiance, temperature regime or soil moisture), and biotic conditions (e.g.  
90 herbivory, seed dispersal or pollination) (Cadenasso & Pickett 2000). Two types of  
91 colonization can be defined, depending on the origin of the species. The colonization  
92 by a species present in the regional species pool, can be defined as an autochthonous  
93 species colonization (Fig. 1-2a), while the colonization by a species absent in the  
94 regional species pool (e.g. invasion by an exotic species or the colonization by a new  
95 species as an effect of changed climatic conditions) can be defined as an allochthonous

96 species colonization (Fig. 1-2b). The number of species only present in the regeneration  
97 layer may complement the future tree layer composition and can therefore be defined  
98 as recruitment credit. For instance, the number of species absent from the mature tree  
99 layer but persistent in a seedling bank can be considered a recruitment credit. These  
100 tree seedlings or saplings can spend decades in the forest understory waiting for  
101 openings in the canopy to provide adequate light for growth in the canopy layer  
102 (Comita, Aguilar, Perez, Lao & Hubbell 2007; Comita & Hubbell 2009; Cruz-  
103 Rodriguez & Lopez-Mata 2004). The recruitment of seedlings and saplings to the life  
104 stage of mature trees depends on multiple stochastic, natural and anthropogenic factors  
105 and can result in successful (Fig. 1-3a) and unsuccessful (Fig. 1-3b) species  
106 recruitment. The quantification of the regenerating pool is a valuable indicator of  
107 potential future tree species composition, and possibly a counterbalancing addition to  
108 the extinction debt (Benítez-Malvido et al. 2003; Hylander & Ehrlén 2013; Kirika et al.  
109 2010).

110

111 Vegetation change can directly be detected by repeated observation of permanent plots  
112 or simulation models can be used to forecast community dynamics (Feeley & Silman  
113 2009; Hubbell, He, Condit, Borda-de-Agua, Kellner et al. 2008; Wearn, Reuman &  
114 Ewers 2012). However, such data is often not available for tropical regions and  
115 expertise is often lacking to run sophisticated models (Jackson et al. 2010). These  
116 approaches are often applied to determine extinction events, yet studies on both  
117 extinction and colonization events are scarce, especially in tropical regions (Comita et  
118 al. 2007; Jackson et al. 2010; Kirika et al. 2010; Metzger et al. 2009; Wearn et al.  
119 2012). We developed and implemented a regional and a local species accounting

120 equation, which allow the evaluation of the current forest composition and the  
121 assessment of potential future dynamics. For instance, the equation includes the  
122 quantification of potential extinction debt, colonization credit and recruitment credit.  
123 The surveys of mature tree, sapling and seedling layer composition were conducted in  
124 82 plots localised in two relatively large, one medium sized and nine very small forest  
125 relicts in Taita Hills, Kenya. A simultaneous ordination of these datasets delivered  
126 insights in community composition dynamics due to potential species extinction,  
127 colonization or recruitment. More specifically we tested the following hypotheses:  
128 (i) Tree species composition differs between life stages, both in large and small forest  
129 relicts.  
130 (ii) The larger forest relicts are characterized by a low potential extinction debt,  
131 recruitment and colonization credit.  
132 (iii) Small forest relicts have a high potential extinction debt and colonization credit  
133 and a low potential recruitment credit.

## 134 **Materials and methods**

### 135 *Study area*

136 The Afromontane forest patches of the Taita Hills are located in southeastern Kenya  
137 (3°20' S, 38°15' E), 150 km inland (Pellikka, Lotjonen, Sijander & Lens 2009). These  
138 hills form the northern terminus of the Eastern Arc Mountains, which are known as a  
139 biodiversity hotspot (Burgess, Butynski, Cordeiro, Doggart, Fjeldsa et al. 2007). The  
140 Taita Hills rise abruptly from the Tsavo plains (600-700 m), reaching 2208 m at Vuria  
141 peak. These semi-arid plains isolate the Taita forests from other mountainous areas, of  
142 which Mount Kasigau is the closest at ca. 50 km distance. The potential natural  
143 vegetation is Afromontane cloud forest thanks to the high rainfall and the moisture-laden  
144 southeast trade winds originating from the Indian Ocean. Located in the inter-tropical  
145 convergence zone, the area has a bimodal rainfall pattern; the long rains occur in March-  
146 May and short rains in November-December. The main concern in the Taita Hills, as in  
147 other parts of the Eastern Arc Mountains, is the loss and degradation of the indigenous  
148 forest (Myers, Mittermeier, Mittermeier, da Fonseca & Kent 2000; Newmark 2008). An  
149 accelerating human population growth during the past 200 years, characterized by  
150 agricultural expansion, fuel wood cutting, logging, livestock grazing and forest burning,  
151 is the major driving force of forest loss. Nowadays, 12 forest relicts remain scattered  
152 across hilltops and ridges. In total, the two larger relicts (>100 ha), one medium-sized  
153 relict (86 ha) and the nine small relicts (<10 ha) cover less than 413 ha (see Appendix A:  
154 Table 1 and Figure 1). The two largest relicts are less affected by anthropogenic  
155 disturbance, while the medium-sized and small forest relicts (hereafter referred to as  
156 small forest relicts), representing 35% of the total indigenous forest area, are currently  
157 threatened by small-scale and low intensity logging and livestock grazing and browsing.



158 The native forest can be characterized as secondary moist montane to intermediate  
159 montane forest with high species dissimilarity between individual relicts (Aerts, Thijs,  
160 Lehouck, Beentje, Bytebier et al. 2011). Despite their small size, these forest patches are  
161 characterized by a unique, highly diverse flora and fauna and by large numbers of  
162 endemic species. For instance, at least 13 plant species are Taita endemics (Brooks,  
163 Mittermeier, Mittermeier, da Fonseca, Rylands et al. 2002).

164

#### 165 *Data collection*

166 In the 12 forest relicts, we located 82 plots (see Appendix A: Table 1 and Figure 1) with  
167 a minimum of two plots per relict. Plots had a nested design, with mature trees (woody  
168 individuals  $\geq 5\text{m}$ ) being identified and counted in  $20\times 20\text{ m}^2$  plots, saplings (woody  
169 individuals  $\geq 1\text{ m}$  and  $< 5\text{ m}$ ) in one  $10\times 10\text{ m}^2$  subplot per plot and seedlings (woody  
170 individuals  $< 1\text{ m}$ ) in five  $1\times 1\text{ m}^2$  subplots per plot. *Psychotria* species were identified  
171 to genus only since neither fruits nor flowers required for species identification were  
172 available. Shrub species were excluded from the analyses because they rarely occur in  
173 the mature tree layer ( $> 5\text{ m}$ ) and impede correct comparisons between the three life  
174 stages. Plant species names follow the Flora of Tropical East Africa.

175

#### 176 *Species community composition change*

177 At landscape level, a multiresponse permutation procedure (MRPP) test was used for  
178 testing the hypothesis of no difference between the three life stages and between the  
179 large and small forest relicts. The test statistic A is given as a descriptor of within  
180 group homogeneity, compared to random expectation. (McCune & Mefford 2002).  
181 Nonmetric multidimensional scaling (NMDS) (McCune & Mefford 1999) was used to  
182 assess the indirect gradients influencing the overall species composition changes at the

183 several forest relicts for the three life stages (seedling, sapling and mature tree). The  
184 ordination was run on the presence-absence dataset using the Sørensen distance  
185 measure, six starting dimensions, 40 iterations and an instability criterion of  $10^{-5}$   
186 (McCune et al. 2002). Species scores were calculated with weighted averaging.  
187 Wilcoxon rank-sum test was used for the pairwise comparison of the length and the  
188 Rayleigh test for the direction of species composition shifts from seedling and sapling  
189 to mature tree layer.

190

#### 191 *Species accounting equations*

192 Both a local ( $N_L$ ) and a regional ( $N_R$ ) species accounting equation were developed. The  
193 former is applicable to a single forest patch or to a subset of forest patches (e.g. in this  
194 study a combination of all the small forest relicts), while the latter is valid for the pool  
195 of all the forest relicts in a specific landscape.

196 For the local species accounting equation ( $N_L$ ), a forest relict is considered that consists  
197 of both regenerating ( $R$ ) and non-regenerating species ( $N$ ).

$$198 \quad N_L = R + N \quad (\text{Eq. 1})$$

199 Regenerating species are species that are present in both the mature tree layer and the  
200 seedling or sapling layer. The sapling layer is included to diminish the chance of  
201 missing some regeneration through a mast year effect (Brearley, Proctor, Suriantata,  
202 Nagy, Dalrymple et al. 2007; Comita et al. 2007). Further, the non-regenerating species  
203 can be split into two groups: mature species without any regeneration (potential  
204 extinction debt or  $D_E$ ) and seedlings or saplings without representatives in the mature  
205 tree layer (potential recruitment credit or  $C_R$ ). Thus, from Eq. 1 it follows that:

$$206 \quad N_L = R + D_E + C_R \quad (\text{Eq. 2})$$

207 Isolated habitat relicts can be colonized, and the species potentially able to arrive  
208 constitute the potential colonization credit ( $C_C$ ). Together with the local species pool, it  
209 represents the regional species pool  $N_R$ , which will be quantified based on the  
210 inventory of 82 plots in this study.

$$211 \quad N_R = N_L + C_C = R + D_E + C_R + C_C \quad (\text{Eq. 3})$$

212 The local species pool  $N_L$  can, therefore, also be calculated as the regional species pool  
213  $N_R$  minus the potential colonization credit:

$$214 \quad N_L = N_R - C_C \quad (\text{Eq. 4})$$

215 The MRPP and ordination were conducted using PC-ORD 5.0 for Windows (McCune et  
216 al. 1999), circular statistics using Oriana 3.21 (Kovach Computing Services, Anglesey,  
217 Wales) and Wilcoxon rank-sum tests were conducted using SPSS 15.0 for Windows  
218 (SPSS Inc., Chicago, IL, USA).

219

## 220 **Results**

### 221 *Tree species composition changes*

222 The NMDS ordination (cumulative explained variance: 67.8%) revealed a different  
223 species composition between the three life stages (Fig. 2). The vectors of these species  
224 composition shifts from both seedling and sapling to mature tree layer are not  
225 significantly different between the small and the large forest relicts (Length: Wilcoxon  
226 rank-sum test:  $U_{sapling} = 3$ ,  $p_{sapling} = 0.13$ ,  $U_{seedling} = 10$ ,  $p_{seedling} = 1.00$ ; Direction:  
227 Rayleigh test:  $Z_{sapling} = 10.74$ ,  $p_{sapling} < 0.001$ ;  $Z_{seedling} = 6.59$ ,  $p_{seedling} < 0.001$ ). The  
228 MRPP test confirmed that the three different forest strata (mature tree, sapling and  
229 seedling) were internally more homogeneous than random expectation, both in large and  
230 small forest relicts ( $A_{small} = 0.055$ ,  $A_{large} = 0.041$ ;  $p < 0.001$ ). The early-successional  
231 species *Albizia gummifera* was positively correlated ( $r_s = 0.577$ ) and the late-  
232 successional species *Cola greenwayi* and *Craibia zimmermannii* were negatively  
233 correlated ( $r_s = -0.519$  and  $-0.558$ ) with the first NMDS dimension. *C. zimmermannii*  
234 was positively correlated with the second NMDS dimension ( $r_s = 0.581$ ), as were the  
235 other late-successional species *Chrysophyllum gorungosanum* ( $r_s = 0.555$ ),  
236 *Garcinia volkensii* ( $r_s = 0.628$ ), *Newtonia buchananii* ( $r_s = 0.622$ ), *Strombosia scheffleri*  
237 ( $r_s = 0.672$ ) and *Strychnos mitis* ( $r_s = 0.574$ ) (see Appendix A: Table 2).

238

### 239 *Solving the species accounting equations*

240 The values for the variables in the regional species accounting equation ( $N_R = R + D_E +$   
241  $C_R + C_C$ ) were calculated based on the inventory of 82 plots. The regional species pool  
242  $N_R$  was 78 species comprising 71 regenerating species R, seven species facing potential  
243 extinction (= extinction debt  $D_E$ ) and no potential recruitment credit  $C_R$ . Assuming an

244 allochthonous species colonization of zero (Fig. 1-2b; no invasion of exotic species or  
245 colonization by new species), the potential colonization credit  $C_C$  was set to zero as, per  
246 definition, the autochthonous colonization on regional level is always zero.

247 The local species accounting equation ( $N_L = R + D_E + C_R$ ) was solved for both the large  
248 ( $n = 47$ ) and small ( $n = 35$ ) forest relicts (Fig. 3). The local species pool  $N_L$  of the large  
249 forest relicts was  $61.0 (\pm 7.1)$  species, comprising  $46.5 (\pm 8.4)$  regenerating species  $R$ , a  
250 potential extinction debt  $D_E$  of  $11.5 (\pm 3.5)$  species and a potential recruitment credit  $C_R$   
251 of  $3.0 (\pm 2.8)$ , while the potential colonization credit  $C_C$  was  $17.0 (\pm 7.0)$ . The local  
252 species pool  $N_L$  of the small forest relicts was  $20.3 (\pm 6.5)$  species, comprising  $10.5$   
253  $(\pm 5.0)$  regenerating species  $R$ , a potential extinction debt  $D_E$  of  $4.1 (\pm 3.0)$  species and a  
254 potential recruitment credit  $C_R$  of  $5.7 (\pm 2.5)$ , while the potential colonization credit  $C_C$   
255 was  $57.7 (\pm 2.5)$ .

256

257 **Discussion**

258 *Extinction and recruitment at landscape level*

259 In this study, 9% of the tree species currently have the potential to become extinct in the  
260 Taita Hills region, which is similar to the extinction rates of 5 – 9% in the tropical  
261 forests of the Amazon Basin (Feeley et al. 2009). However, this is substantially less  
262 than the 20 – 30% range reported in Panama (Comita et al. 2007) and Brazil (Hubbell et  
263 al. 2008). A common characteristic of species facing extinction is that they occur in low  
264 densities and in a small range, which is typical for many tropical species (Benítez-  
265 Malvido et al. 2003; Laurance et al. 2006). Therefore, protection and extension of the  
266 remaining habitats are necessary to maintain viable populations of these species (Fahrig  
267 2002; Gibson et al. 2011; Hill & Curran 2001). The regional recruitment credit of zero  
268 implies that no long-distance colonization by indigenous species occurred in the Taita  
269 Hills forests in recent years.

270

271 *Species composition in forest relicts*

272 As observed in other tropical forests (Farwig et al. 2008; Hill et al. 2001; Laurance et al.  
273 2006; Lawes et al. 2007), several early-successional species dominate the mature tree  
274 layer of the smallest relicts. The large-scale logging of valuable timber trees (e.g.  
275 *Ocotea usambarensis* and *Podocarpus latifolius*) in the past and the large-scale  
276 conversion of indigenous forest to farmland have created gaps and edges, in which were  
277 subsequently colonized by light-demanding (e.g. *A. gummifera* and *Macaranga*  
278 *capensis*), disturbance-tolerant (e.g. *Tabernaemontana stapfiana*) or edge-associated  
279 species (*Maesa lanceolata*) (Comita et al. 2007; Kirika et al. 2010). Bussmann (2001)  
280 found similar successional trajectories and regeneration patterns for other montane

281 forests of Kenya (e.g. Mount Kenya, Mt Nyiru) and Ethiopia (e.g. Menagesha forest).  
282 Conversely, the large relicts still harbor a large portion of late-successional species,  
283 most likely because natural regeneration of these species was less disturbed.

284

285 *Dynamics in forest relicts*

286 The implementation of the local species accounting equation offered ecological insights  
287 into the potential future mature species composition (i.e. regenerating mature trees and  
288 the potential recruitment credit;  $R + C_R$ ) of Taita Hills. Our approach is preferable to the  
289 conventional approaches, which are often exclusively based on mature tree species  
290 composition (i.e. all mature trees, irrespective of their regeneration status;  $R + D_E$ )  
291 (Hubbell et al. 2008; Metzger et al. 2009; Ramos, Simonetti, Flores & Ramos-Jiliberto  
292 2008). For Taita Hills, the conventional approach results in an average species richness  
293 of 58 and 15 species for the larger and smaller forest relicts, respectively, whereas our  
294 species accounting approach, which takes potential extinction and recruitment into  
295 account, predicts less species for large fragments (49.5) and more species for small  
296 fragments (16.2). Both large and small relicts are expected to lose approximately 20%  
297 of their current tree species pool. However, a gradual recovery of the small, severely  
298 degraded forest relicts, a successful colonization and negative density-dependent  
299 recruitment of seedlings may mitigate species loss in the small relicts (Comita et al.  
300 2009; Harms, Wright, Calderon, Hernandez & Herre 2000). The fact that almost 30% of  
301 the species pool in small forest relicts is currently only present in the regeneration layer  
302 may be an early signal of such species recovery (Comita et al. 2007). These specimens  
303 may originate from a seed bank, from mature trees that died afterwards or from other  
304 forest relicts through seed dispersal (Farwig et al. 2008; Kirika et al. 2010; Moran,  
305 Catterall & Kanowski 2009).

306

307 *Species accounting equation performance*

308 To our knowledge, the species accounting equation is a novel approach to assess the  
309 current and future forest relict composition. The advantage of this tool is the integration  
310 of the regeneration layer, while many studies (e.g. forest health monitoring projects or  
311 conservation plans) are often solely based on the mature tree layer. The inclusion of the  
312 regeneration layer and, more specifically, the subdivision of the mature species pool in  
313 regenerating and non-regenerating species provide a nuanced assessment of the forest  
314 conservation status. The equation is straightforward, which offers an additional  
315 advantage, especially in the context of participatory monitoring (Holck 2008). A single  
316 inventory is sufficient to solve the equations, and such surveys are feasible by basic  
317 untrained observers (Holck 2008; Robinson & Lokina 2012).

318

319 Extinction debt, recruitment and colonization credit are much more developed,  
320 theoretically and mathematically, than their implementation in the species accounting  
321 equations (Jackson et al. 2010). Extinction calculations remain difficult due to unknown  
322 complex biological responses or interactions and uncertain future land cover changes,  
323 which can affect species-specific survival and reproduction rates (Feeley et al. 2009;  
324 Hubbell et al. 2008; Mendenhall, Daily & Ehrlich 2012). In our approach, species  
325 without regeneration are considered as species with a higher potential to become  
326 extinct, especially when no recruits are seen in both the seedling and the sapling layer,  
327 although the possibility remains that they regenerate during particular times or under  
328 special environmental conditions. However, the risk of extinction remains extremely



329 high in small forest relicts, because stochastic or anthropogenic events can suddenly  
330 eradicate the remaining mature populations of a particular species.

331 Future autochthonous colonizations are difficult to predict because not all sites may be  
332 suitable for the regeneration of each species from the regional species pool. In our  
333 approach, the potential colonization credit represents the maximum potential  
334 autochthonous colonization credit and it does not assume that all these species can  
335 effectively colonize a patch. In fragmented landscapes and degraded forests such as in  
336 the Taita Hills, dispersal and recruitment limitation may substantially limit effective  
337 colonization. In this context, the implementation of the concept of ‘dark diversity’ can  
338 be considered, which is the portion of the regional species pool potentially able to occur  
339 in a forest relict (Pärtel, Szava-Kovats & Zobel 2011). This would lead to a potential  
340 colonization credit, which is the sum of (i) dark diversity or *real* colonization credit and  
341 (ii) species that will fail to colonize a relict. This approach requires additional tree trait  
342 data (e.g. dispersal capacity or competitiveness and site requirements), environmental  
343 data (e.g. species-specific site suitability) and geographical data (e.g. spatial  
344 configuration of relicts, distances and physical barriers between relicts). Finally, the  
345 potential recruitment credit represents the potential species pool that can enter the  
346 mature tree layer. Also these recruits may face several deterministic and stochastic  
347 processes. For instance, pathogenic fungi, herbivores, water stress, nutrient or light  
348 limitation and mechanical damage due to falling branches and leaves can hamper the  
349 seedling growth and sapling recruitment to the life stage of mature trees (Comita et al.  
350 2009; Cruz-Rodriguez et al. 2004; Harms et al. 2000). It is almost impossible to study  
351 seedling recruitment to the adult stage directly, especially for late-successional tree  
352 species, which often survive in seedling banks until a gap is created in the forest canopy

353 (Farwig et al. 2008). In our observational study, we solved this problem by adopting a  
354 stage-for-time approach, which meant including specimens in the sapling stage (i.e.  
355 trees between 1 to 5 m) as representatives of the past seedling stage, i.e. specimens that  
356 regenerated and survived for several years to decades (Connell & Green 2000). This  
357 sapling pool functioned as an indicator of initial successful seedling recruitment to the  
358 life stage of mature trees.

359

### 360 *Conservation of forest relicts*

361 There is ambiguity about the conservation value of small forest relicts (Zhu, Xu, Wang  
362 & Li 2004), but in the Taita Hills, the large tree species diversity in the regeneration  
363 layer highlights their conservation potential. The regeneration layer is critical for forest  
364 persistence (Lawes et al. 2007) and a successful recruitment of these species into the  
365 mature tree layer may enable the small forest relicts to develop into forest communities  
366 that are more similar to undisturbed forests. If human activities that affect tree  
367 recruitment are addressed (Aschero & Garcia 2012; Ramirez-Marcial 2003), the small  
368 forest relicts of the Taita Hills could contribute to the regional conservation of  
369 Afromontane cloud forest biodiversity.

370

371 **Acknowledgments**

372 We are obliged to the Kenyan government for authorizing research in Taita Hills  
373 (NCST/RRI/12/1/MAS/66). We wish to thank G. Mungai, D. Kimuzi, F. Watoli and  
374 J. Kikuvi for field assistance; T. Callens, V. Lehouck and T. Spanhove for sharing their  
375 expertise about the region; and the Taita Research Station of the University of Helsinki  
376 for their hospitality. K. Hylander, K. Hövemeyer and the anonymous reviewers are  
377 gratefully acknowledged for their useful comments. This study was supported by a  
378 Research Foundation Flanders grant (G.0055.08) and a University of Leuven FLOF  
379 grant to K.W.T. We declare that we have no conflicts of interest with our sponsors.

380

381 **Appendix A. Supplementary data**

382

383 Supplementary data associated with this article can be found, in the online version, at  
384 XXXXX.

385

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520 its ecological and species diversity changes in southern Yunnan. *Biodiversity and*  
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524

525 **Figure legends**

526

527 **Fig. 1.** Conceptual figure representing the current ( $T_0$ ) and future ( $T_{+1}$ ) tree species  
528 composition of a forest relict under different scenarios (hypothetical example). The  
529 event is represented in bold in each scenario, while for the other specimens the status is  
530 kept constant. See Table 1 for calculation examples based on this figure.

531

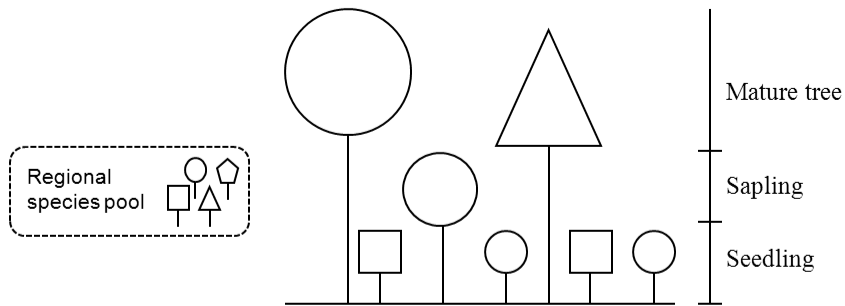
532 **Fig. 2.** Non-metric multidimensional scaling (NMDS) ordination of the plot data (246  
533 records = 82 plots  $\times$  3 life stages per plot) from 12 forest relicts in the Taita Hills,  
534 Kenya. NMDS ordination was performed simultaneously for three life stages but results  
535 are presented separately for mature trees (A), saplings (B) and seedlings (C). The  
536 NMDS ordination scores are averaged for each forest relict. Two large, less disturbed  
537 forest relicts are presented in black ( $\bullet$ ); ten smaller, disturbed forest relicts are shown in  
538 white ( $\circ$ ). NMDS dimension 1 and 2 explained 28.6% and 22.3% of the variance,  
539 respectively. Panel (D) shows species vectors for seven late-successional species (#1-7)  
540 and one early-successional tree species (#8). Only species that were significantly  
541 correlated with at least one NMDS dimension are shown.

542

543 **Fig. 3.** The relative proportion (%) of regenerating species ( $R$ ), potential extinction debt  
544 ( $D_E$ ) and potential recruitment credit ( $C_R$ ) for two large forest relicts and ten small forest  
545 relicts of Taita Hills, Kenya.

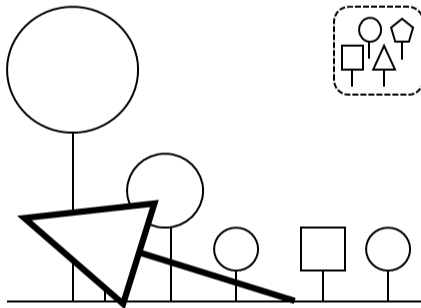
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**Current forest composition ( $T_0$ )**

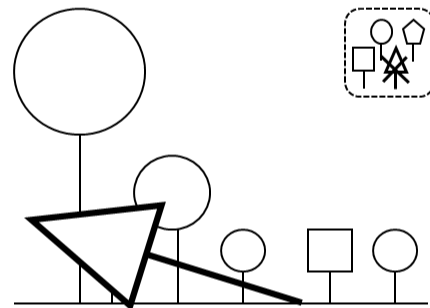


**Future forest composition ( $T_{+1}$ )**

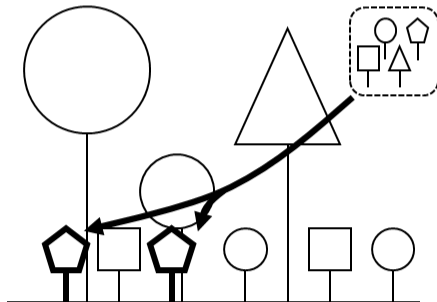
Scenario 1a: **Local species extinction**



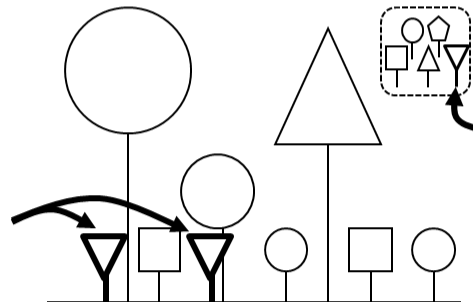
Scenario 1b: **Regional species extinction**



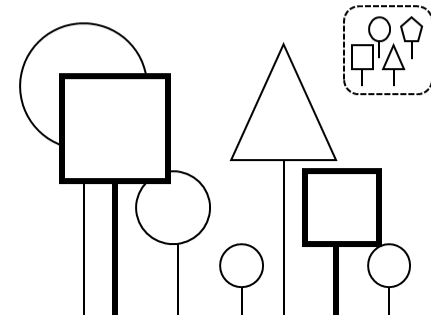
Scenario 2a: **Autochthonous colonization**



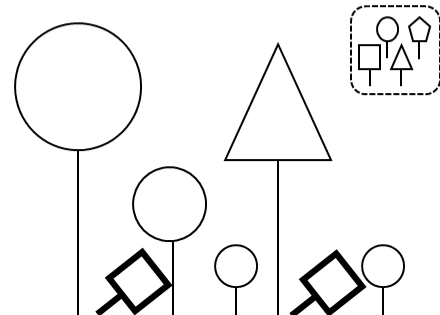
Scenario 2b: **Allochthonous colonization**



Scenario 3a: **Successful species recruitment**



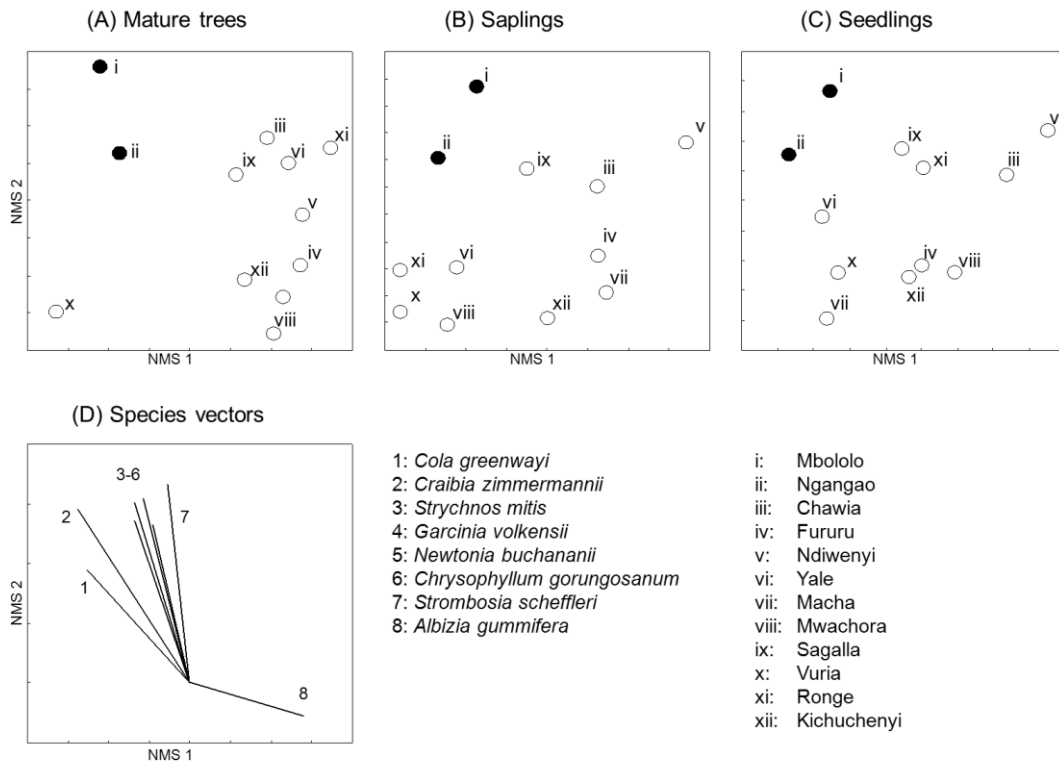
Scenario 3b: **Failure species recruitment**



547

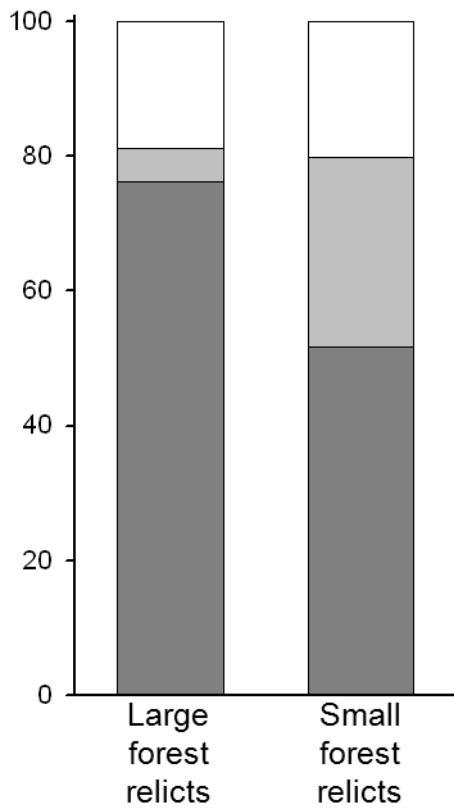
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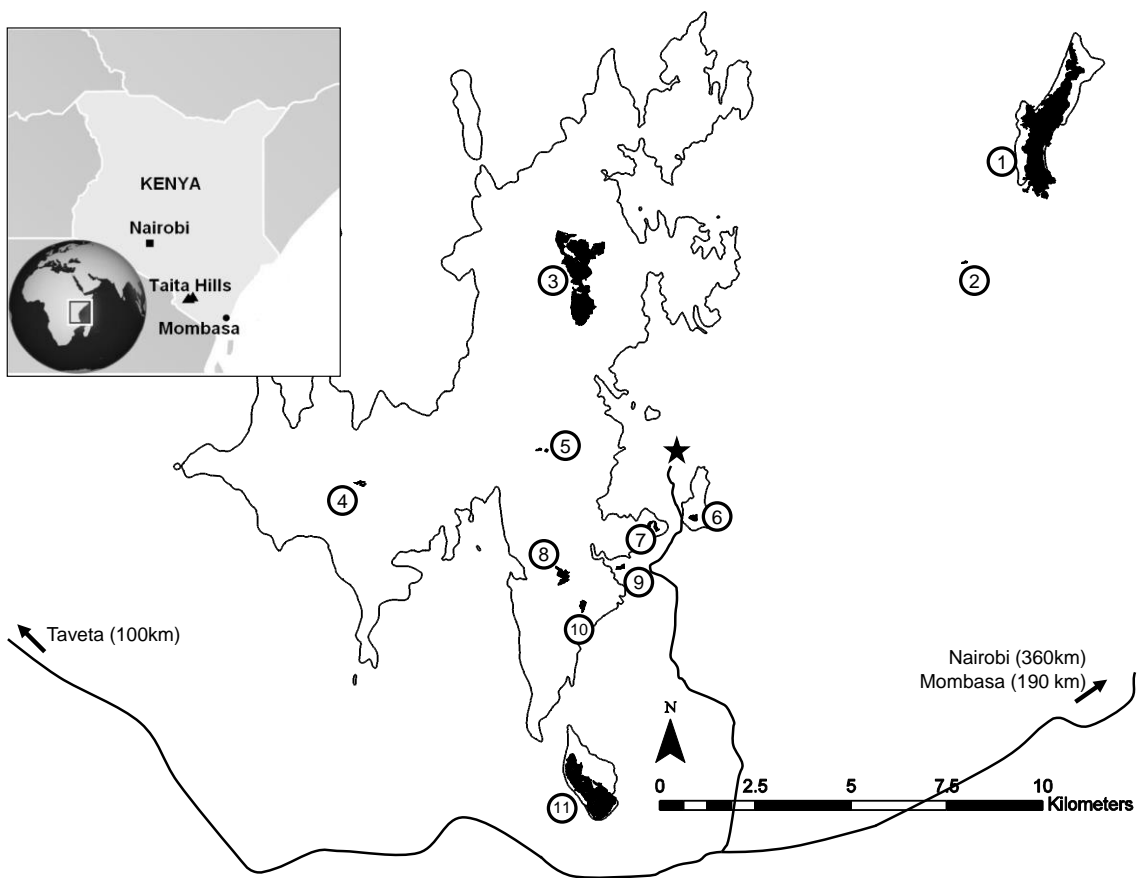
- Potential extinction debt
- ▒ Potential recruitment credit
- Regenerating species



550

551 **Appendix A: Fig. 1.** Map of the study area indicating the geographical position in  
 552 Kenya and the location of the twelve indigenous forest relicts of Taita Hills, Taita  
 553 Taveta District, Kenya (forest relict Sagalla falls outside the figure boundary). 1-  
 554 Mbololo, 2-Ronge, 3-Ngangao, 4-Vuria, 5-Yale, 6-Mwachora, 7-Macha, 8-Fururu, 9-  
 555 Kichuchenyi, 10-Ndiwenyi, 11-Chawia. The grey contour line is at 1500 m altitude and  
 556 the black star is the location of the town Wundanyi.

557



558

559

560 **Appendix A: Table 1.** Relevant information of the 12 indigenous forest relicts of Taita

561 Hills

Forest	Area (ha)	Number of plots	Elevation (m)	Coordinates	Description
Mbololo	185	30	1400-1800	03°19'S 38°27'E	Largest and most intact forest relict, only <i>Saintpaulia teitensis</i> B.L.Burt
Ngangao	120	17	1750-1900	03°21'S 38°20'E	Located on an eastern slope of a north-south oriented mountain ridge with very steep slopes; indigenous forest mixed with plantation forest, surrounded by agricultural land and only <i>Meineckia ovata</i> E.A. Bruce
Chawia	86	14	1500-1600	03°28'S 38°20'E	Southernmost, heavily disturbed forest located on gentle slopes; plantations of exotic trees interspersed by agricultural land
Fururu	8	5	1650-1750	03°25'S 38°20'E	Partly disturbed forest relict with patches of small remnant in the east and one in the south
Ndiwenyi	3	2	1600	03°26'S 38°20'E	Heavily disturbed forest relict and surrounded by agricultural land
Yale	2	2	1850	03°24'S 38°20'E	Two small forest relicts; located on the east-west oriented mountain ridge with very steep slopes and surrounded by agricultural land with plantations.
Macha	2	2	1600	03°25'S 38°21'E	Located on a west-east oriented ridge; disturbed forest interspersed by agricultural land and plantation
Mwachora	2	2	1650	03°25'S 38°22'E	East of Macha; located on steep hilltop; disturbed forest interspersed by agricultural land
Sagalla	2	2	1450-1500	03°30'S 38°35'E	Narrow strip of forest which receives more rainfall than the other forest relicts; surrounded by agricultural land; located on the isolated Mount Sagalla, 25 km to the south of the other relicts
Vuria	1	2	2200	03°24'S 38°17'E	Highest peak (2208m) and the westernmost forest relict; small forest relict of closed canopy forest; the surrounding environment is heavily disturbed and has a high degree of fragmentation

Ronge	1	2	1300	03°21'S 38°25'E	Low riverine forest located near a stream; plantations
Kichuchenyi	1	2	1450	03°25'S 38°22'E	South of Macha and Mwachora; smallest as Josa; heavily disturbed and surrounded

562

563

564

565 **Appendix A: Table 2.** Species list containing the most relevant species, sorted on the  
566 relative frequency of their basal area (BA). Spearman rank correlations ( $r_s$ ) between  
567 NMDS plot scores and the species occurrence are shown. Significant correlations ( $p <$   
568  $0.05$ ) with  $|r_s| > 0.5$  are shown in bold. For each species, its increase ( $\uparrow$ ), decrease ( $\downarrow$ ) or  
569 no change ( $\leftrightarrow$ ) in abundance in the regeneration layer in comparison with the mature  
570 tree layer is shown (column a). Species threatened by potential regional extinction or  
571 species with a potential recruitment credit are represented by  $D_E$  or  $C_R$ , respectively  
572 (column b)

573

BA	Scientific name	Family	Habit	$r_s$ NMDS axis 1	$r_s$ NMDS axis 2	a	b
11.3 %	<i>Albizia gummifera</i>	Mimosaceae	Upper-canopy tree	<b>0.577</b>	-0.141	$\downarrow$	
9.6 %	<i>Tabernaemontana stapfiana</i>	Apocynaceae	Understorey tree	0.434	0.020	$\downarrow$	$C_R$
9.3 %	<i>Newtonia buchananii</i> <sup>3</sup>	Mimosaceae	Upper-canopy tree	-0.241	<b>0.622</b>	$\leftrightarrow$	
8.7 %	<i>Macaranga capensis</i>	Euphorbiaceae	Canopy tree	0.276	0.116	$\downarrow$	
6.7 %	<i>Cola greenwayi</i> <sup>1,3</sup>	Sterculiaceae	Canopy tree	<b>-0.519</b>	0.376	$\uparrow$	$C_R$
5.8 %	<i>Millettia oblata</i> <sup>2</sup>	Papilionaceae	Canopy tree	0.073	-0.273	$\downarrow$	$C_R$
5.2 %	<i>Polyscias fulva</i>	Araliaceae	Canopy tree	0.210	-0.013	$\downarrow$	
4.2 %	<i>Craibia zimmermannii</i> <sup>3</sup>	Papilionaceae	Canopy tree	<b>-0.558</b>	<b>0.581</b>	$\leftrightarrow$	
3.7 %	<i>Chrysophyllum gorungosanum</i> <sup>3</sup>	Sapotaceae	Canopy tree	-0.196	<b>0.555</b>	$\uparrow$	
3.4 %	<i>Maesa lanceolata</i>	Myrsinaceae	Shrub or tree	0.279	-0.232	$\leftrightarrow$	
2.7 %	<i>Syzygium guineense</i>	Myrtaceae	Upper canopy tree	0.399	-0.196	$\leftrightarrow$	$C_R$
2.7 %	<i>Strombosia scheffleri</i> <sup>3</sup>	Olaceae	Understorey tree	-0.119	<b>0.672</b>	$\leftrightarrow$	
1.7 %	<i>Leptonychia usambarensis</i>	Sterculiaceae	Understorey tree	0.046	0.038	$\leftrightarrow$	$C_R$
1.6 %	<i>Psychotria sp.</i>	Rubiaceae	Shrub or tree	-0.315	-0.160	$\uparrow$	$C_R$
1.5 %	<i>Phoenix reclinata</i>	Palmae	Understorey - canopy	0.380	-0.310	$\downarrow$	
< 1%	<i>Cussonia spicata</i>	Araliaceae	Upper-canopy tree	0.247	-0.250	$\downarrow$	
< 1%	<i>Canthium oligocarpum</i>	Rubiaceae	Shrub or tree	-0.022	-0.041	$\leftrightarrow$	$C_R$
< 1%	<i>Aphloia theiformis</i>	Aphloiaceae	Understorey tree	-0.118	-0.051	$\leftrightarrow$	$C_R$
< 1%	<i>Rytigynia uhligii</i>	Rubiaceae	Shrub or tree	0.037	-0.315	$\leftrightarrow$	$C_R$
< 1%	<i>Garcinia volkensii</i> <sup>3</sup>	Guttiferae	Canopy tree	-0.300	<b>0.628</b>	$\leftrightarrow$	$C_R$
< 1%	<i>Pauridianta paucinervis</i>	Rubiaceae	Shrub or tree	-0.318	0.209	$\leftrightarrow$	$C_R$
< 1%	<i>Lasianthus kilimandscharicus</i>	Rubiaceae	Shrub or tree	-0.027	0.328	$\leftrightarrow$	$C_R$
< 1%	<i>Bersama abyssinica</i>	Melianthaceae	Shrub or tree	0.046	-0.056	$\leftrightarrow$	$C_R$

< 1%	<i>Teclea nobilis</i>	Rutaceae	Canopy tree	-0.024	0.018	↔	C <sub>R</sub>
< 1%	<i>Vangueria volkensii</i>	Rubiaceae	Shrub or tree	0.119	-0.357	↑	C <sub>R</sub>
< 1%	<i>Ficus exasperata</i>	Moraceae	Canopy tree	0.023	0.040	↓	C <sub>R</sub>
< 1%	<i>Lepidotrichilia volkensii</i> <sup>1</sup>	Meliaceae	Canopy tree	0.039	-0.238	↔	C <sub>R</sub>
< 1%	<i>Strychnos mitis</i> <sup>3</sup>	Loganiaceae	Understorey tree	-0.298	<b>0.574</b>	↔	
< 1%	<i>Rauvolfia mannii</i>	Apocynaceae	Shrub or tree	-0.253	-0.148	↑	C <sub>R</sub>
< 1%	<i>Clausena anisata</i>	Rutaceae	Shrub or tree	0.058	-0.371	↑	C <sub>R</sub>
< 1%	<i>Cremaspora triflora</i>	Rubiaceae	Understorey tree	-0.127	0.276	↓	D <sub>E</sub>
< 1%	<i>Ehretia cymosa</i>	Boraginaceae	Shrub or tree	-0.024	-0.125	↔	
< 1%	<i>Ficus sur</i>	Moraceae	Canopy tree	0.126	0.011	↓	D <sub>E</sub>
< 1%	<i>Ficus sycomorus</i>	Moraceae	Canopy tree	0.139	-0.011	↓	D <sub>E</sub>
< 1%	<i>Ilex mitis</i>	Aquifoliaceae	Shrub or tree	-0.047	0.129	↓	D <sub>E</sub>
< 1%	<i>Maesopsis eminii</i>	Rhamnaceae	Canopy tree	0.129	-0.062	↔	
< 1%	<i>Nuxia congesta</i>	Loganiaceae	Shrub or tree	-0.007	0.122	↓	D <sub>E</sub>
< 1%	<i>Ouratea schusteri</i> <sup>1</sup>	Ochnaceae	Understorey tree	-0.035	0.136	↓	D <sub>E</sub>
< 1%	<i>Schefflera myrianta</i>	Araliaceae	Liana, shrub or tree	0.033	-0.140	↓	D <sub>E</sub>

574 <sup>1</sup> Eastern Arc Mountain endemic species

575 <sup>2</sup> Taita Hills endemic species

576 <sup>3</sup> Late-successional species which we found in the regeneration layer of the small forest relicts. All  
577 these species are strongly affiliated with the large, intact forest relicts

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