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1 **Woody plant communities of isolated Afromontane cloud forests in Taita**
2 **Hills, Kenya**

3

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14

15

1 **Abstract**

2 In the Taita Hills in southern Kenya, remnants of the original Afromontane forest
3 vegetation are restricted to isolated mountain peaks. To assess the level of
4 degradation and the need for forest restoration, we examined how forest plant
5 communities and their indicator species vary between and within remnant patches of
6 cloud forest. We used ordinal abundance data to compare plant communities in
7 eight forest fragments. We also analyzed data on the diversity and abundance of
8 trees in 57 0.1 ha plots to compare tree communities within and between the largest
9 two of these fragments, Ngangao (120 ha) and Mbololo (220 ha). The extant
10 vegetation of the Taita Hills at landscape scale consists of secondary moist montane
11 to intermediate montane forest. There was a high species dissimilarity between
12 fragments (69%). Variation in species composition coincided with an abiotic gradient
13 related to elevation. At plot level, secondary successional species and species of
14 forest edges were most abundant and most frequent. Inferred clusters of plots
15 almost entirely coincided with the two forest fragments. Indicator species associated
16 with forest margins and gaps were more frequent in the smaller of the two forest
17 fragments, while indicators for the larger fragment were more typical for less
18 disturbed moist forest. Abiotic site variability but also different levels of disturbance
19 determine site-specific variants of the montane forest. Conservation efforts should
20 not only focus on maintaining forest quantity (size), but also on forest quality (species
21 composition). Late-successional rainforest species are underrepresented in the
22 woody plant communities of the Taita Hills and assisting restoration of viable
23 populations of cloud forest climax tree species is urgently needed.

24

25 **Key words**

26 Eastern-Arc Mountains, Fragmentation, Montane forest, *Ocotea*, Taita Hills, Relict
27 vegetation

28

1 **Introduction**

2 Habitat loss and climate change pose increasing threats for biological
3 communities worldwide (Thomas et al. 2004; Ewers and Didham 2006). In
4 Africa, patterns of biodiversity and human population show remarkable
5 similarity, and this often causes land use conflicts (Balmford et al. 2001;
6 Fjeldså and Burgess 2008; Lewis 2009). In particular, forests are at stake:
7 from 2000 to 2005 the continent lost about 4 million hectares of forest
8 annually, close to one-third of the area deforested globally (FAO 2009). With
9 these forests, many plant communities and their associated fauna and
10 ecosystem services are being lost (Lewis 2009).

11 Deforestation affects biological forest communities in various ways.
12 Cutting forest reduces the amount of habitat, isolates the remaining patches
13 (habitat fragmentation) and alters the local or regional microclimate (Lawton et
14 al. 2001; Fahrig 2003). In remaining forest fragments, selective logging (Berry
15 et al. 2008; Ruger et al. 2008) and the subsequent invasion of alien or early-
16 successional species (Devlaeminck et al. 2005; Heckmann et al. 2008) further
17 degrade habitat quality. Consequently, biological communities in fragmented
18 forests are expected to differ from the original, pre-fragmentation situation
19 (temporal effect). They are also expected to vary between and within
20 remaining forest patches.

21 Abiotic site conditions are responsible for natural variation of vegetation
22 patterns. In disturbed ecosystems, processes such as soil erosion may affect
23 abiotic site conditions, for instance through nutrient losses (de Koff et al.
24 2006). Differences in size, shape and degree of disturbance may have
25 additional effects on the vegetation (spatial effect). Species in the altered

1 communities may facilitate, tolerate or inhibit the recruitment of the original
2 climax species. The invasion of forest clearings by *Pteridium aquilinum*
3 (Bracken fern) and the subsequent arrested succession is a typical example
4 of inhibition (e.g. Rodrigues Da Silva and Matos 2006). Ecological restoration
5 must therefore acknowledge the present site potential and the remaining
6 vegetation, because both may pose constraints for restoring plant
7 communities.

8 In this study, we investigate the variation in forest plant communities in
9 an extremely fragmented Afromontane cloud forest in the Taita Hills, southern
10 Kenya. The Taita Hills form the northeastern part of the Eastern Arc
11 Mountains, a mountain range with an exceptionally high degree of endemism
12 and conservation value (Myers et al. 2000; Burgess et al. 2007; Hall et al.
13 2009). Because of favorable climate and soil, most of the forests of the Taita
14 Hills have been cleared for agriculture more than 100 years ago (Pellikka et
15 al. 2009). Consequently, existing forest fragments have been isolated from
16 one another and embedded in agricultural rural landscape for over 100 years
17 (Newmark 1998; Pellikka et al. 2009). At present only three relatively large
18 forest patches (86–200 ha) and less than ten small forest patches (< 1–16 ha)
19 remain. With the purpose of conserving and restoring Afromontane cloud
20 forest in southern Kenya, the primary objectives of this paper are to identify
21 forest plant communities of the Taita Hills and their indicator species. We
22 compare species lists of different forest fragments accumulated over a long
23 time period to assess the potential natural vegetation at landscape level. We
24 then compare recent survey data within two large forest patches to evaluate if

1 the present plant communities still represent the potential natural vegetation,
2 and to evaluate local species composition variability.

3

4 **Methods**

5 *Study sites*

6 The Taita Hills forests (3°25'S, 38°20'E) are located in southeast Kenya, 25
7 km west of Voi in the Taita-Taveta District (Fig. 1). The Taita Hills rise
8 abruptly from the semi-arid Tsavo plains at 600-700 m to a series of ridges,
9 reaching 2208 m at Vuria peak. The plains isolate the hills from other
10 mountains and highland blocks, the closest being Mount Kasigau (ca. 50 km
11 to the southeast), North Pare (ca.70 km southwest), Mount Kilimanjaro (ca.
12 110 km west) and the West Usambara mountains (ca.120 km south) (Birdlife
13 International 2007).

14 Rainfall follows a bimodal pattern alternated with a long (June–
15 September) and a short (February) dry period (Lehouck et al. 2009b). The
16 area receives between 600 mm and 2300 mm rainfall per year. Precipitation
17 varies between years and locations, decreasing from east to west (Beentje
18 and Ndiang'ui 1988; Lehouck et al. 2009b). Moist forest in the Taita Hills
19 depends on cloud precipitation brought in by southeast trade winds originating
20 from the Indian Ocean (Beentje and Ndiang'ui 1988). Cloud forests are
21 restricted to sites receiving over 900 mm of annual precipitation. In the Taita
22 hills, such sites are located above 1400 m altitude on the southeastern slopes
23 and above 1700 m altitude on the northwestern slopes (Pellikka et al. 2009).

24 Indigenous forest fragments are found on two isolated hills and a main
25 massif. The isolated hills are Mount Sagalla and Mbololo Hill. The patch on

1 Mount Sagalla is located at an altitude between 1350 and 1450 m. On
2 Mbololo Hill, at 1200-1750 m, one of the three larger fragments (Mbololo,
3 indigenous forest area 220 ha) and two very small patches occur (a patch
4 within Ronge plantation, < 1 ha; a patch near Mwabirwa forest station, < 1
5 ha). The massif is known as Dabida Hill, with an elevation of 1400–2200 m.
6 Forest patches on Dabida Hill included in this study are Ngangao (120 ha),
7 Chawia (86 ha), Yale (16 ha) and Vuria (< 1 ha). Ngangao is located on a
8 steep eastern slope of a north-south oriented ridge at 1700–1952 m. Chawia
9 is located at the top of a cliff and has gentle slopes between 1470 and 1600
10 m. Yale is located on a north-south oriented mountain ridge with very steep
11 slopes between 1750 and 2104 m (Pellikka et al. 2009). Five other forest
12 fragments in the Dabida massif were not included in this study because
13 compatible vegetation data were not available (Fururu, 8 ha; Macha, 3 ha;
14 Mwachora, 2 ha; Ndiwenyi, < 1 ha; Kichuchenyi, < 1ha). All fragments are
15 partly to heavily disturbed, mixed with or surrounded by plantation forest of
16 exotic species (including *Eucalyptus saligna*, *Pinus patula*, *Cupressus*
17 *lusitanica*, *Grevillea robusta* and *Acacia mearnsii*). The landscape matrix
18 consists of smallholder agricultural land, where coffee, mangoes, cassava,
19 tomatoes, banana, maize and beans are the main crops (Beentje and
20 Ndiang’ui 1988; Bytebier 2001; Pellikka et al. 2009).

21

22 *Data collection*

23 We used ordinal abundance data to compare species composition of eight
24 forest fragments. We also analyzed data on the diversity and abundance of

1 trees in 57 0.1 ha plots to compare tree communities within and between the
2 largest two of these fragments.

3 For the comparison between fragments, we used species lists of all
4 higher plants recorded in the forests of Taita Hills between 1877 and 1985
5 (Faden et al. 1988). More rare and vagrant species may be included in
6 species lists compiled over long periods and thus, differences in composition
7 between locations may be weakened. Therefore, we assume that these data
8 are most useful at landscape scale. It is also the only existing reference for
9 the assessment of the potential natural vegetation. Species occurring only
10 outside the forests were not taken into account. Forest fragments included in
11 the species list were the larger fragments Mbololo, Ngangao and Chawia, the
12 smaller fragment Yale, and the patches of Vuria, Mwabirwa, Ronge and
13 Sagalla. Frequency symbols in Faden et al. (1988) followed a modified
14 Tansley scale ((locally) abundant, (locally) common, frequent, uncommon and
15 rare) and were converted to presence/absence data. This transformation
16 meant losing information about relative abundances, but allowed for
17 calculating distance measures. For analysis of woody plant communities, we
18 used trees (100 species), woody climbers (6 species) and shrubs (46
19 species).

20 For the comparison within and between the two largest forest
21 fragments (Mbololo and Ngangao), we used woody species data from a
22 recent survey (Mbuthia 2003). Trees and palms measuring ≥ 10 cm diameter
23 at 1.30 m height were recorded in 57 sample plots. The plots measured 50 x
24 20 m² and were laid out along stratified random east-west transects in
25 Mbololo (26 plots) and Ngangao (31 plots) (Mbuthia 2003). The relative

1 importance values recorded by Muthia (2003) were the average of the
2 relative frequency, relative density and relative basal area of a species in
3 percent. These scores were converted to presence/absence data. After
4 omitting 11 unidentified species that occurred only in a single plot each, 73
5 woody species were retained for further analysis.

6 Plant species names follow the Flora of Tropical East Africa. Primary
7 sources for plant species information (autoecology) were Beentje (1994),
8 Maundu et al. (2005) and the African Plants Initiative (www.aluka.org).

9

10 *Data analysis*

11 We used the Sørensen dissimilarity index to evaluate pairwise differences in
12 species composition between forests fragments (species list data). Mantel
13 statistics were used to relate differences in species composition between
14 fragments to geographical distances. Forest fragments were clustered into
15 groups using a Sørensen distance measurement and flexible beta linkage (β
16 = -0.25) (McCune and Mefford 1999). Indicator Species Analysis (Dufrêne
17 and Legendre 1997) was applied to calculate indicator values for all species
18 and their significance for the emerging groups. Homogeneity within groups
19 was tested with a multiresponse permutation procedure (MRPP) test. For
20 MRPP, we used the Sørensen distance measure and a natural group
21 weighing factor $n_i/\sum n_i$ (where n_i is the number of samples in each group). In
22 MRPP, the chance-corrected within group agreement A describes within-
23 group homogeneity compared to random expectation. If the emerging groups
24 are significantly more homogeneous than expected by chance, then $1 > A > 0$
25 (McCune and Mefford 1999). Non-metric multidimensional scaling (NMS)

1 based on the Sørensen distance measure, which is the most appropriate
2 method for community analysis, was used to investigate indirect gradients
3 influencing species distribution (Faith et al. 1987; Minchin 1987). We first
4 removed outlier species (by use of a cut-off point of two standard deviations
5 from the grand mean Sørensen distance measure). NMS was run using six
6 starting dimensions, 40 iterations, an instability criterion of 10^{-5} and a rotation
7 for maximum variance (McCune and Mefford 1999). Community composition
8 was compared to species lists of the different forest types of Kenya (Beentje
9 1990; Trapnell 1997; Kindt et al. 2007).

10 We also used the Sørensen dissimilarity index and NMS to evaluate
11 pairwise differences in species composition between plots (plot data). Plots
12 were clustered into groups. Indicator values for all species and their
13 significance were calculated for the emerging groups. Homogeneity within
14 groups was tested with a multiresponse permutation procedure (MRPP) test.
15 We used the same procedures as those described for fragments. Before
16 analysis, four outlier plots (including two plots near a water tank and a school)
17 were omitted from the dataset.

18 Classification, ordination and statistical tests were conducted using PC-
19 ORD 5.0 for Windows (McCune and Mefford 1999) and SPSS 15.0 for
20 Windows (SPSS Inc., Chicago, IL).

21

22 **Results**

23 *Plant communities at landscape scale*

24 There was a high species dissimilarity between the forest fragments (overall
25 mean Sørensen dissimilarity 69%). Floristic dissimilarities (Sørensen

1 distances between fragments) were not related to geographical (Euclidian)
2 distances between fragments (Mantel $r = -0.230$, $P = 0.345$).

3 Clustering the fragments in three groups provided the most informative
4 number of clusters, with more homogeneity within groups than expected by
5 chance (MRPP $A = 0.18$, $P = 0.013$). Three woody species communities were
6 identified, containing 19 to 126 species: remnants of riverine forest (Mwabirwa
7 and Ronge), high altitude forest remnants (Vuria and Yale), and moist
8 montane forests (Sagalla, Chawia, Ngangao and Mbololo) (Table 1).

9 For the NMS ordination, the best solution was two-dimensional (final
10 stress 0.002, mean stress in real data 7.94, $P = 0.004$). The ordination
11 isolated the high altitude forest remnants from the other fragments along one
12 axis and the other two communities along a second axis. Within communities,
13 individual fragments occupied nearly identical positions in the two-dimensional
14 space of the ordination (Fig. 2).

15

16 *Plant communities at patch scale*

17 Eight species were found in more than 50% of all plots (overall relative
18 frequency > 0.5): *Tabernaemontana stapfiana* (relative frequency 0.88),
19 *Macaranga conglomerata* (0.81), *Strombosia scheffleri* (0.73), *Craibia*
20 *zimmermannii* (0.69), *Newtonia buchananii* (0.65), *Albizia gummifera* (0.62),
21 *Rapanea melanophloeos* (0.58) and *Syzygium sclerophyllum* (0.56). These
22 species also had the highest relative importance values in both forests (Fig.
23 3), indicating that plant communities of both forest fragments are dominated
24 by a few widespread species.

1 There was a high species dissimilarity between the two forest fragments
2 (Sørensen dissimilarity 64%). Clustering the plots into two groups almost
3 perfectly coincided with the separation between the two forests. A first group
4 comprised all but one plot in Ngangao plus five plots from the southern edge
5 of Mbololo. The second group comprised most plots of Mbololo (minus the
6 five plots in the south) and a single plot in the center of Ngangao. The groups
7 showed a high species dissimilarity (67%) and were more homogenous within
8 groups than can be expected by chance (MRPP $A = 0.09$, $P < 0.001$). For the
9 NMS ordination, the best solution was two-dimensional (final stress 25.52,
10 mean stress in real data 27.26, $P = 0.004$). Ngangao forest was clearly
11 separated from Mbololo in the two-dimensional space of the ordination (Fig. 4,
12 white symbols versus black symbols). Similarly, both plant communities were
13 separated in the ordination (Fig. 4, circles versus triangles). The species with
14 the highest, significant indicator values for the first group (most of Ngangao
15 and south Mbololo) included three species associated with forest margins and
16 edges and disturbance. The indicators for the second group (most of
17 Mbololo) were more typical for less disturbed moist forest (Table 2).

18

19 **Discussion**

20 *Natural vegetation of the Taita Hills*

21 Results of this study (species list data) show that the potential natural
22 vegetation of the Taita Hills consists of moist montane forest. The natural
23 moist montane forest type is *Ocotea* forest, which is also known as upland
24 rainforest (Greenway 1973), Afromontane rainforest (White 1983) and
25 *Ocotea-Podocarpus* forest (Lind and Morrison 1974). It has strong affinities

1 with that of other mountain isolates in the Eastern Arc Mountains (Beentje and
2 Ndiang'ui 1988; Lovett 1993). Within Kenya, forest communities that share
3 keystone species with the Taita Hills forests are found on (mainly south and
4 southeast) slopes and peaks at Mount Kasigau, Machakos Hills, Ol Doinko
5 Sabuk, Kiangombe, the Aberdares (Nyeri), Mount Kenya, Mukinduri,
6 Nyambeni, Mau, Tinderet Peak and Cherangani Hills (see Beentje 1990 for a
7 description of these forests). These forests are *Ocotea* and *Newtonia* forests,
8 or *Pouteria (Aningeria)-Strombosia-Drypetes* forest and *Albizia-Neoboutonia-*
9 *Polyscias* forest. The latter two forest types can be seen as degraded and
10 marginal variants of *Ocotea* forest (Beentje 1990).

11

12 *Plant communities at landscape scale*

13 At the landscape level (species list data), the different isolated forest
14 fragments in the Taita Hills are characterized by one plant community despite
15 the relatively large barriers between the different peaks. Based on the
16 indicator species (Table 1), the forest type can be identified as (secondary)
17 moist montane to intermediate montane forest. In Taita Hills, this forest type
18 is represented on the four main peaks (Mbololo, Ngangao, Chawia and
19 Sagalla). The keystone species, *Ocotea usambarensis* and *Podocarpus*
20 *latifolius*, have been extracted for timber in the past and now only occur in
21 small diameter classes (Bytebier 2001; Mbutia 2003). Vuria and Yale may
22 be high altitude, degraded variants. These small fragments show poorer
23 structural quality, species richness and diversity than the larger fragments
24 (Wilder et al. 1998; Chege and Bytebier 2005; Githiru et al. 2005). The
25 patches at Mwabirwa and Ronge are two special variants at lower altitude

1 representing riparian phases of the montane forest community – not because
2 all lower altitude forest types would be riparian forest types, but because the
3 only natural vegetation left in these fragments was located at wetter sites.

4

5 *Plant communities at patch scale*

6 Differentiation of the plant communities between the two largest forest
7 remnants in the Taita Hills, Mbololo and Ngangao, may be related to
8 differences in abiotic site conditions or precipitation. However, the distribution
9 of indicator species over both fragments show that different levels of
10 anthropogenic disturbance may have contributed too (Table 2). In Ngangao,
11 the tree species with the highest relative importance (*T. stapfiana*, *M.*
12 *conglomerata* and *A. gummifera*; Fig. 3) are early-successional species
13 typical of edges and gaps. These species are also important in Mbololo, but
14 two other species (*S. scheffleri* and *N. buchananii*; Fig. 3) have the highest
15 importance. These species are not typically associated with disturbance, but
16 neither with primary cloud forest. Low evenness (strong dominance of few
17 species) and indicator species suggest that both forests are disturbed, but
18 Mbololo forest is less disturbed than Ngangao forest (see also Wilder et al.
19 1998).

20

21 *Potential causes for high dissimilarity between communities*

22 The high dissimilarity between the Taita Hills forest fragments may be an
23 effect of historical or recent isolation. The Taita Hills have been isolated at
24 the landscape scale (the Eastern Arc Mountains) and on a geological time
25 scale (290–180 M yr BP). Isolation could have shaped the plant communities

1 when comparing the Taita Hills to other mountain isolates. Within the Taita
2 Hills, the role of historical isolation is less evident. The Taita Hills may have
3 been covered by continuous cloud forest (Pellikka et al. 2009), but detailed
4 information about pre-disturbance forest cover is insufficient to conclude that
5 historical isolation has shaped the plant communities of individual fragments.

6 More recently, the efficiency of seed dispersal of different tree species
7 between fragments has decreased. These species are experiencing
8 difficulties in maintaining stable populations in all forest fragments (Cordeiro et
9 al. 2009; Lehouck et al. 2009a; Lehouck et al. 2009c). This implies that some
10 fragments could have an extinction debt (Tilman et al. 1994). As habitat
11 quality deteriorates some tree species will eventually become locally extinct
12 after repeated failure of recruitment (Lehouck et al. 2009b). This is expected
13 to occur sooner in small than in large fragments. Depending on what species
14 will go extinct, this process may further increase or rather decrease pairwise
15 differences between fragments. As highly sensitive and specialized species
16 are more susceptible to local extinction, future extinctions may lead to biotic
17 homogenisation and increased dominance by generalist or early-successional
18 species (Lewis 2009).

19

20 *Implications for conservation*

21 While at the landscape level, the potential natural vegetation of the Taita Hills
22 is moist montane forest, secondary species and species of gaps and edges
23 are dominating the remnant vegetation. The various degraded states of the
24 fragments require adapted management strategies. In the most degraded
25 forests, restoring a form of secondary forest as an interim nurse stand may be

1 a more realistic method than trying to restore pristine *Ocotea* forest
2 immediately (see also Wright and Muller-Landau 2006). Such a restoration
3 may already be ongoing in stands of planted trees surrounding the fragments
4 of indigenous forests. The planted trees may facilitate the recruitment of
5 native forest trees by acting as safe sites for seedlings (see e.g. Chapman
6 and Chapman 1996; Lemenih and Teketay 2005; Zamora and Montagnini
7 2007). In other cases, planting or sowing indigenous trees may be needed to
8 diversify impoverished forests or species-poor plantations (Aerts et al. 2006;
9 Aerts et al., 2009). Planted trees may attract seed-dispersing animals (Elliot
10 et al. 2003) and can act as a nurse crop for more demanding tree species by
11 providing shade and improving soil conditions (Farwig et al. 2009).

12 Conservation-related intervention in the Taita Hills is urgent because
13 only a small area of the forests remains (Brooks et al. 1998; Rogo and Oguge
14 2000). To preserve the biological richness of the Taita Hills, and in broader
15 perspective, of the Eastern Arc, it is necessary to conserve indigenous forest
16 over its entire elevation range (Hall et al. 2009). In the Taita Hills, this means
17 conserving all indigenous forest fragments, including the very small and
18 degraded patches. But conservation efforts should not only focus on
19 maintaining forest quantity (size and number of patches), but also on forest
20 quality (species composition). Species of old-growth cloud forest, such as
21 *Ocotea usambarensis*, *Pouteria adolfi-friederici* and *Podocarpus latifolius* are
22 underrepresented in the communities of the Taita Hills. Assisting restoration
23 of viable populations of such cloud forest climax tree species is urgently
24 needed.

25

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9

1 **References**

- 2 Aerts R., Maes W.H., November E., Negussie A., Hermy M. and Muys B.
3 2006. Restoring dry Afromontane forest using bird and nurse plant effects:
4 direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and*
5 *Management* 230: 23-31.
- 6 Aerts R., Volkaert H., Roongruangsree N., Roongruangsree U.-T., Swennen
7 R. and Muys B. 2009. Site requirements of the endangered rosewood
8 *Dalbergia oliveri* in a tropical deciduous forest in northern Thailand. *Forest*
9 *Ecology and Management* 259: 117-123.
- 10 Balmford A., Moorje J.L., Brooks T., Burgess N., Hansen L.A., Williams P. and
11 Rahbek C. 2001. Conservation conflicts across Africa. *Science* 291: 2616-
12 2619.
- 13 Beentje H.J. 1990. The forests of Kenya. *Mitteilungen aus dem Institut für*
14 *Allgemeine Botanik in Hamburg* 23a: 265-286.
- 15 Beentje H.J. 1994. Kenya trees, shrubs, and lianas. National Museums of
16 Kenya, Nairobi.
- 17 Beentje H.J. and Ndiang'ui N. 1988. Ecology of the forests. In: Beentje H.J.
18 (ed), *An ecological and floristic study of the forests of the Taita Hills, Kenya.*
19 *Utafiti Occasional Papers of the National Museums of Kenya* 1: 1-42.
- 20 Berry N.J., Phillips O.L., Ong R.C. and Hamer K.C. 2008. Impacts of selective
21 logging on tree diversity across a rainforest landscape: the importance of
22 spatial scale. *Landscape Ecology* 23: 915-929.

1 BirdLife International 2007. Taita Hills forests. BirdLife's online World Bird
2 Database: the site for bird conservation V 2.1. Cambridge, UK (Available at
3 www.birdlife.org, accessed 17/4/2008, archived at
4 www.webcitation.org/5YlvE7k2A).

5 Brooks T., Lens L. , Barnes J., Barnes R., Kihuria J.K. and Wilder C. 1998.
6 The conservation status of the forest birds of Taita Hills, Kenya. *Bird
7 Conservation International* 8: 119-139.

8 Burgess N.D., Butynski T.M., Cordeiro N.J., Doggart N.H., Fjeldså J., Howell
9 K.M., Kilahama F.B., Loader S.P., Lovett J.C., Mbilinyi B., Menegon M.,
10 Moyer D.C., Nashanda E., Perkin A., Rovero F., Stanley W.T. and Stuart S.N.
11 2007. The biological importance of the Eastern Arc Mountains of Tanzania
12 and Kenya. *Biological Conservation* 134: 209-231.

13 Bytebier B. 2001. Taita Hills Biodiversity Project Report. National Museums of
14 Kenya, Nairobi, Kenya.

15 Chapman C.A. and Chapman L.J. 1996. Exotic tree plantations and the
16 regeneration of natural forests in Kibale National Park, Uganda. *Biological
17 Conservation* 76: 253-257.

18 Chege J. and Bytebier B. 2005. Vegetation structure of four small forest
19 fragments in Taita Hills, Kenya. *Journal of East African Natural History* 94:
20 231-234.

21 Cordeiro N.J., Ndangalasi H.J., Mcentee J.P. and Howe H.F. 2009. Disperser
22 limitation and recruitment of an endemic African tree in a fragmented
23 landscape. *Ecology* 90: 1030-1041.

- 1 de Koff J.P., Graham R.C., Hubbert K.R. and Wohlgemuth P.M. 2006. Prefire
2 and postfire erosion of soil nutrients within a chaparral watershed. *Soil*
3 *Science* 171: 915-928.
- 4 Devlaeminck R., Bossuyt B. and Hermy M. 2005. Inflow of seeds through the
5 forest edge: evidence from the seed bank and vegetation patterns. *Plant*
6 *Ecology* 176: 1-17.
- 7 Duf r ne M. and Legendre P. 1997. Species assemblages and indicator
8 species: the need for a flexible asymmetrical approach. *Ecological*
9 *Monographs* 67: 345-366.
- 10 Elliott S., Navakitbumrung P., Kuarak C., Zangkum S., Anusarnsunthorn V.
11 and Blakesley D. 2003. Selecting framework tree species for restoring
12 seasonally dry tropical forests in Northern Thailand based on field
13 performance. *Forest Ecology and Management* 184: 177-191.
- 14 Ewers R.M. and Didham R.K. 2006. Confounding factors in the detection of
15 species responses to habitat fragmentation. *Biological Reviews* 81: 117-142.
- 16 Faden R.B., Beentje H.J. and Nyakundi D.O. 1988. Checklist of the forest
17 plant species. In: Beentje H.J. (ed), *An ecological and floristic study of the*
18 *forests of the Taita Hills, Kenya*. Utafiti Occasional Papers of the National
19 *Museums of Kenya* 1: 43-66.
- 20 Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual*
21 *Review of Ecology Evolution and Systematics* 34: 487-515.
- 22 Faith D.P., Minchin P.R. and Belbin L. 1987. Compositional dissimilarity as a

1 robust measure of ecological distance. *Vegetatio* 69: 57-68.

2 FAO. 2009. State of the world's forests 2009. Food and Agriculture
3 Organization, Rome.

4 Farwig N., Sajita N. and Bohning-Gaese K. 2009. High seedling recruitment of
5 indigenous tree species in forest plantations in Kakamega Forest, Western
6 Kenya. *Forest Ecology and Management* 257: 143-150.

7 Fjeldså J. and Burgess N.D. 2008. The coincidence of biodiversity patterns
8 and human settlement in Africa. *African Journal of Ecology* 46: 33-42.

9 Githiru M., Bennun L., Lens L. and Ogot C.P.K.O. 2005. Spatial and temporal
10 variation in fruit and fruit-eating birds in the Taita Hills, southeast Kenya.
11 *Ostrich* 76: 37-44.

12 Greenway P.J. 1973. A classification of the vegetation of East Africa. *Kirkia* 9:
13 1-68.

14 Hall J., Burgess N.D., Lovett J., Mbilinyi B. and Gereau R.E. 2009.
15 Conservation implications of deforestation across an elevational gradient in
16 the Eastern Arc Mountains, Tanzania. *Biological Conservation* 142: 2510-
17 2521.

18 Heckmann K.E., Manley P.N. and Schlesinger M.D. 2008. Ecological integrity
19 of remnant montane forests along an urban gradient in the Sierra Nevada.
20 *Forest Ecology and Management* 255: 2453-2466.

21 Kindt R., van Breugel P. and Barnekow Lillesø J.-P. 2007. Use of vegetation
22 maps to infer on the ecological suitability of species using central and western

1 Kenya as an example. Part II: Tree species lists for potential natural
2 vegetation types. Forest & Landscape Denmark and World Agroforestry
3 Centre, Hørsholm, Denmark and Nairobi, Kenya.

4 Lawton R.O., Nair U.S., Pielke R.A. and Welch R.M. 2001. Climatic impact of
5 tropical lowland deforestation on nearby montane cloud forests. *Science* 294:
6 584-587.

7 Lehouck V., Spanhove T., Colson L., Adringa-Davis A., Cordeiro N.J. and
8 Lens L. 2009a. Habitat disturbance reduces seed dispersal of a forest interior
9 tree in a fragmented African cloud forest. *Oikos* 118: 1023-1034.

10 Lehouck V., Spanhove T., Gonsamo A., Cordeiro N. and Lens L. 2009b.
11 Spatial and temporal effects on recruitment of an Afromontane forest tree in a
12 threatened fragmented ecosystem. *Biological Conservation* 142: 518-528.

13 Lehouck V., Spanhove T., Vangestel C., Cordeiro N.J. and Lens L. 2009c.
14 Does landscape matrix affect resource tracking by avian frugivores in a
15 fragmented Afrotropical forest? *Ecography* 32: 789.

16 Lemenih M. and Teketay D. 2005. Effect of prior land use on the
17 recolonization of native woody species under plantation forests in the
18 highlands of Ethiopia. *Forest Ecology and Management* 218: 60-73.

19 Lewis O.T. 2009. Biodiversity change and ecosystem function in tropical
20 forests. *Basic and Applied Ecology* 10: 97-102.

21 Lind E.M. and Morrison M.E.S. 1974. *East African vegetation*. Longman,
22 London.

- 1 Lovett J.C. 1993. Eastern Arc moist forest flora. In: Lovett J.C. and Wasser
2 S.K. (eds), Biogeography and ecology of the rain forests of East Africa.
3 Cambridge University Press, Cambridge, pp. 33-35.
- 4 Maundu P.M., Tengnäs B. and Birnie A. 2005. Useful trees and shrubs for
5 Kenya. World Agroforestry Centre, Nairobi, Kenya.
- 6 Mbuthia K.W. 2003. Ecological and ethnobotanical analyses for forest
7 restoration in the Taita Hills, Kenya. Diss. Ph.D. Department of Botany, Miami
8 University, Oxford, Ohio, U.S.A.
- 9 McCune B. and Mefford M.J. 1999. PC-ORD 5.0 for Windows. Multivariate
10 analysis of ecological data. MjM Software, Gleneden Beach, Oregon, U.S.A.
- 11 Minchin P.R. 1987. An evaluation of the relative robustness of techniques for
12 ecological ordination. *Vegetatio* 69: 89-107.
- 13 Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A.B. and Kent J.
14 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- 15 Newmark W. 1998. Forest area, fragmentation and loss in the Eastern Arc
16 Mountains: implications for the conservation of biological diversity. *Journal of*
17 *East African Natural History* 87: 29-36.
- 18 Pellikka P.K.E., Lotjonen M., Sijander M. and Lens L. 2009. Airborne remote
19 sensing of spatiotemporal change (1955-2004) in indigenous and exotic forest
20 cover in the Taita Hills, Kenya. *International Journal of Applied Earth*
21 *Observation and Geoinformation* 11: 221-232.
- 22 Rodrigues Da Silva U.D.S. and Matos D.M.D.S. 2006. The invasion of

1 *Pteridium aquilinum* and the impoverishment of the seed bank in fire prone
2 areas of Brazilian Atlantic Forest. *Biodiversity and Conservation* 15: 3035-
3 3043.

4 Rogo L. and Oguge N. 2000. The Taita Hills forest remnants: a disappearing
5 World Heritage. *Ambio* 29: 522-523.

6 Ruger N., Williams-Linera G., Kissling W.D. and Huth A. 2008. Long-term
7 impacts of fuelwood extraction on a tropical montane cloud forest.
8 *Ecosystems* 11: 868-881.

9 Thomas C.D., Cameron A., Green R.E., Bakkenes M., Beaumont L.J.,
10 Collingham Y.C., Erasmus B.F.N., De Siqueira M.F., Grainger A., Hannah L.,
11 Hughes L., Huntley B., Van Jaarsveld A.S., Midgley G.F., Miles L., Ortega-
12 Huerta M.A., Peterson A.T., Phillips O.L. and Williams S.E. 2004. Extinction
13 risk from climate change. *Nature* 427: 145-148.

14 Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction
15 and the extinction debt. *Nature* 371: 65-66.

16 Trapnell C.G. 1997. Biodiversity and conservation of the indigenous forests of
17 the Kenya highlands. Sansom and Company, Bristol, U.K.

18 White F. 1983. The vegetation of Africa. UNESCO, Paris.

19 Wilder C., Brooks T. and Lens L. 1998. Vegetation structure and composition
20 of the Taita Hills forests. *Journal of East African Natural History* 87: 181-187.

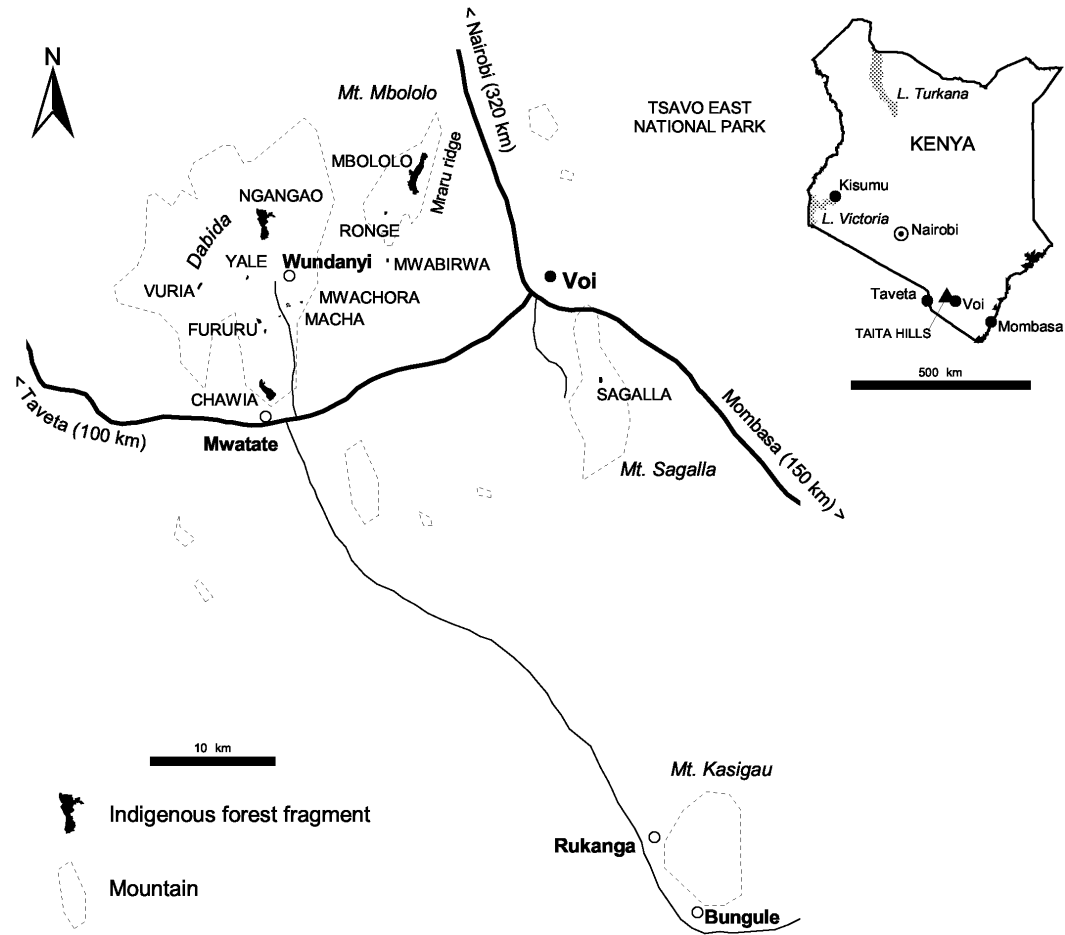
21 Wright S.J. and Muller-Landau H.C. 2006. The future of tropical forest
22 species. *Biotropica* 38: 287-301.

- 1 Zamora C.O. and Montagnini F. 2007. Seed rain and seed dispersal agents in
- 2 pure and mixed plantations of native trees and abandoned pastures at La
- 3 Selva Biological Station, Costa Rica. *Restoration Ecology* 15: 453-461.

4

1 **Figures**

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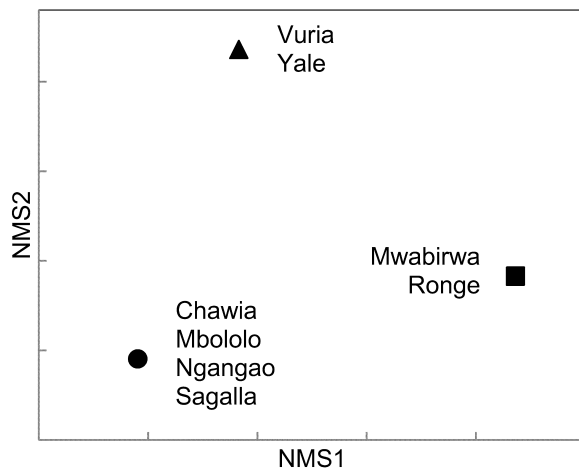
5 **Fig. 1** Forest fragments in the Taita Hills, Taita Taveta District, Kenya.

6 Source data for boundaries, roads, contour lines, cities and lakes © ILRI 2007

7 (available from www.ilri.org/gis)

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4 **Fig. 2** Nonmetric multidimensional scaling (NMS) ordination of eight forest

5 fragments in the Taita Hills, Kenya. Fragments are labeled according to

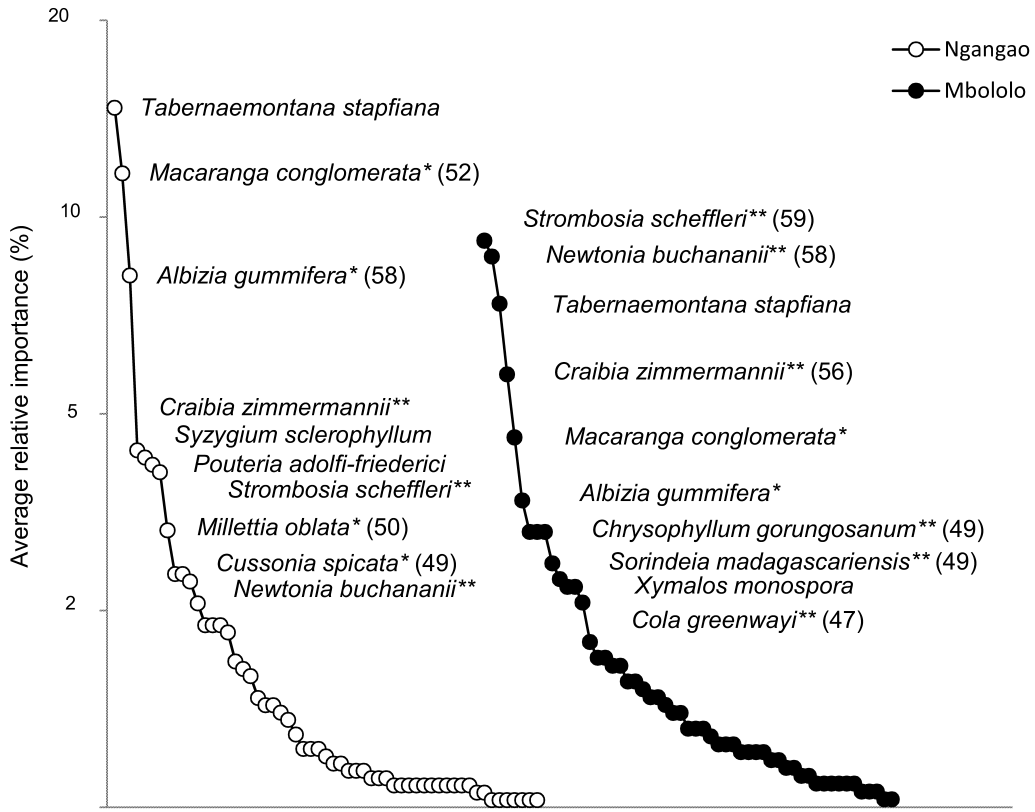
6 woody plant species communities produced by cluster and indicator species

7 analysis: moist montane forest (●), high altitude forest remnants (▲), and

8 remnants of riverine forest (■)

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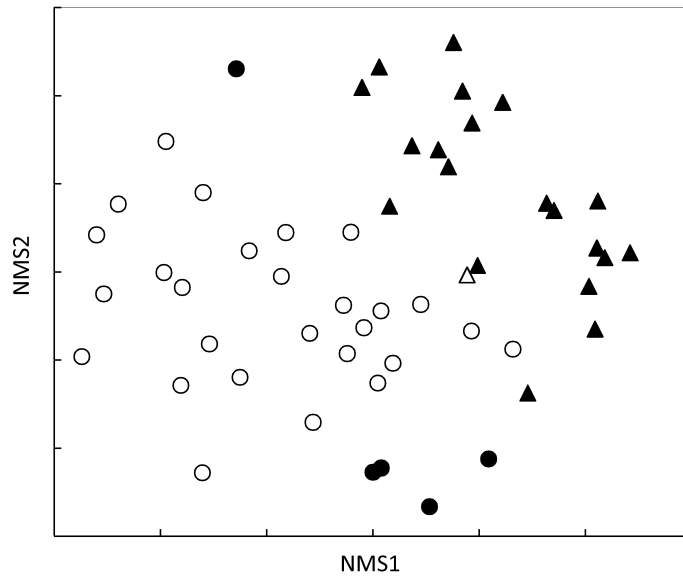


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4 **Fig. 3** Rank-abundance curves of tree communities of moist montane forest
5 in Taita Hills, southern Kenya. Curves are drawn for two fragments, Ngangao
6 and Mbololo. Steep curves indicate low evenness of species. Species
7 followed by indicator values (in parentheses) are significant indicator species
8 ($P < 0.05$) for woody species communities determined by cluster and indicator
9 species analysis: * Community I, ** Community II. Indicator values range from
10 zero (no indication) to 100% (perfect indication). Species are ranked
11 according to relative importance (only the first ten species are labeled).

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3 **Fig. 4** Nonmetric multidimensional scaling (NMS) ordination of 53 plots in
 4 Mbololo forest (black) and Ngangao forest (white) in the Taita Hills, Kenya.
 5 Shapes indicate woody plant species communities produced by cluster and
 6 indicator species analysis: Community I (circles), Community II (triangles)
 7 (see Table 2).

8

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Table 1

Important species of forest communities of woody species in eight isolated forest fragments in Taita Hills, southeast Kenya, determined by indicator species analysis

Indicator species	IV	P	Habit	Habitat
<u>Moist montane forests (Sagalla, Chawia, Ngangao, Mbololo; 126 species)</u>				
<i>Tiliacora funifera</i>	100.0	0.013	Liana	Moist and riverine forest
<i>Chassalia parviflora</i>	100.0	0.013	Shrub	Moist forest
<i>Ochna holstii</i>	100.0	0.013	Subcanopy tree	Dry forest (remnants), mist forest
<i>Craibia zimmermannii</i>	100.0	0.013	Canopy tree	Mist forest
<i>Landolphia buchananii</i>	100.0	0.013	Liana	Riverine and moist forest
<i>Cola greenwayi</i>	100.0	0.013	Canopy tree	Moist forest
<i>Newtonia buchananii</i>	100.0	0.013	Canopy tree	Riverine and moist forest
<i>Tabernaemontana stapfiana</i>	100.0	0.013	Canopy tree	Moist forest; common in disturbed forest
<i>Strombosia scheffleri</i>	66.7	0.073	Canopy tree	Moist forest
<i>Nuxia floribunda</i>	66.7	0.073	Tree	Forest (drier types) or forest remnants
<i>Rauvolfia mannii</i>	66.7	0.073	Shrub or tree	Moist forest, especially in margins and disturbed sites
<i>Syzygium sclerophyllum</i>	66.7	0.073	Canopy tree	Moist forest, mist forest
<i>Macaranga conglomerata</i>	66.7	0.073	Understorey tree	Moist forest; early-successional species in forest margins
<i>Keetia gueinzii</i>	66.7	0.073	Liana	Moist forest and forest margins, secondary bushland, riverine

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Table 1

(continued)

Riverine forests fragments (Mwabirwa, Ronge plantation: 19 species)

<i>Anthocleista grandiflora</i>	80.0	0.138	Canopy tree	Along rivers in forest areas
<i>Macaranga capensis</i>	80.0	0.138	Understorey tree	Moist forest, especially near streams

High altitude forest fragments (Vuria, Yale: 27 species)

<i>Prunus africana</i>	57.1	0.215	Canopy tree	Moist forest
<i>Philippia pallidiflora</i>	57.1	0.409	Tree	Rocky forest edges

Indicator values (IV) range from zero (no indication) to 100% (perfect indication). *P*-values are calculated from a Monte Carlo permutation test for each species. For moist montane forest, only species with an indicator *P*-value < 0.10 are shown. For the other two communities, all indicator *P*-values were > 0.10; only species with the highest IV for each community are shown.

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Table 2

Important species of forest communities of woody species in Ngangao and Mbololo in Taita Hills, southeast Kenya, determined by indicator species analysis

Indicator species	IV	P	Habit	Habitat
<u>Community I (Most of Ngangao and southern edge in Mbololo, n = 32)</u>				
<i>Albizia gummifera</i>	57.6	0.001	Canopy tree	Dry or moist forest (margins), riverine forest
<i>Cussonia spicata</i>	48.8	0.001	Tree	Moist and dry forest and forest margins, riverine forest; early-successional
<i>Macaranga conglomerata</i>	52.2	0.070	Understorey tree	Early-successional tree in edges of wet montane forest
<i>Maesa lanceolata</i>	38.9	0.018	Shrub or tree	Moist forest
<i>Millettia oblata</i>	50.0	< 0.001	Canopy tree	Moist forest (subsp. <i>teitensis</i> , endemic to Taita hills)
<i>Oxyanthus speciosus</i>	40.6	0.002	Shrub or tree	Moist forest
<i>Polyscias fulva</i>	46.9	0.001	Tree	Moist forest, riverine forest
<u>Community II (Most of Mbololo except southern edge and one plot in Ngangao, n = 21)</u>				
<i>Bequaertiodendron natalense</i>	53.8	< 0.001	Canopy tree	Moist mixed evergreen forest
<i>Chrysophyllum gorungosanum</i>	49.1	< 0.001	Canopy tree	Moist forest
<i>Coffea fadenii</i>	37.7	0.007	Understorey tree	Understorey of moist forest; endemic to Mbololo forest
<i>Cola greenwayi</i>	46.9	0.009	Understorey tree	Evergreen forest
<i>Craibia zimmermannii</i>	55.8	0.008	Canopy tree	Moist forest
<i>Diphasiopsis fadenii</i>	42.1	0.001	Shrub or tree	Moist forest
<i>Ilex mitis</i>	19.0	0.022	Shrub or tree	Evergreen mountain forest
<i>Maytenus acuminata</i>	28.6	0.003	Shrub or tree	Moist forest, especially with <i>Ocotea</i>
<i>Newtonia buchananii</i>	58.3	0.004	Canopy tree	Riverine forest, moist forest

<i>Nuxia congesta</i>	23.4	0.043	Shrub or tree	Forest and woodland; common where disturbed
<i>Ocotea usambarensis</i>	23.8	0.008	Canopy tree	Moist forest
<i>Pleiocarpa pycnantha</i>	44.7	< 0.001	Shrub or tree	Wide range
<i>Psychotria crassipetala</i>	38.1	< 0.001	Shrub or tree	Moist forest; endemic to Taita Hills
<i>Sorindeia madagascariensis</i>	49.1	< 0.001	Canopy tree	Riverine forest
<i>Strombosia scheffleri</i>	58.7	0.003	Canopy tree	Moist forest
<i>Strychnos henningsii</i>	51.5	< 0.001	Shrub tree	Dry forest, riverine
<i>Syzygium guineense</i>	28.6	0.002	Large tree	Mountain rainforest

1 Indicator values range from zero (no indication) to 100% (perfect indication). *P*-values are calculated from a Monte Carlo permutation test for each species.

2 Only species with an indicator *P*-value < 0.05 are shown.