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

Running title: Potential tree species shifts in forest relicts

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Abstract

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

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

Introduction

Destruction and loss of natural habitat are major causes of biodiversity decline and species extinction (Brose 2011; Fahrig 2002; Tilman, May, Lehman & Nowak 1994). Forests are one of the largest terrestrial biomes and are severely threatened by anthropogenic habitat deterioration with an estimated loss of 13 to 20 million hectares each year, of which one third is located in the tropics (FAO 2011; Hansen, Potapov, Moore, Hancher, Turubanova et al. 2013). Many plant populations strive to survive in small forest relicts (Ewers & Didham 2006) and the succession of tree species in these forest patches is a central theme in plant community ecology, restoration, and land management (Cook, Yao, Foster, Holt & Patrick 2005).

The succession within these forest relicts is driven by three major events, which can alter the species composition of forest relicts: extinction, colonization and the recruitment of seedlings and saplings to the mature tree layer. In forests, there is a time-lagged response of species to habitat modifications (Hylander & Nemomissa 2009; Jackson & Sax 2010; Metzger, Martensen, Dixo, Bernacci, Ribeiro et al. 2009), because of the long life span and regeneration time of trees (Vellend, Verheyen, Jacquemyn, Kolb, Van Calster et al. 2006). The future extinction of a species due to events that happened in the past is known as delayed extinction and quantified as extinction debt (Hylander et al. 2009; Jackson et al. 2010; Tilman et al. 1994). Although only the preservation of large areas of primary forest can safeguard the complete species pool (Gibson, Lee, Koh, Brook, Gardner et al. 2011), a substantial number of forest species can survive for a long time in small and degraded forest relicts before they become extinct (Helm, Hanski & Pärtel 2006; Kuussaari, Bommarco, Heikkinen, Helm, Krauss et al. 2009; Vellend et al. 2006). Especially the failure of species regeneration is a threat to future forest biodiversity and composition because species persistence depends on the availability of seeds, seedlings and saplings (Albrecht, Neuschulz & Farwig 2012; Benítez-Malvido & Martínez-Ramos 2003; Farwig, Sajita, Schaab & Böhning-Gaese 2008; Lawes, Joubert, Griffiths, Boudreau & Chapman 2007). The extinction of a species that remains present in the regional species pool (local species extinction, Fig. 1-1a), can be counterbalanced by a recolonization of this species from the regional species pool (autochtonous colonization, Fig. 1-2a). However, when a species is present in one relict only, its extinction in this patch will result in the disappearance of the species from the region (regional species extinction, Fig. 1-1b). Colonization credit is the number of species yet to colonize a forest relict (Jackson et al. 2010; Piqueray, Cristofoli, Bisteau, Palm & Mahy 2011). Such establishment of species within forest relicts is a gradual process because it depends on several external factors like landscape structure and ability of newly arrived seeds to germinate, or internal factors like succession or management (Kirika, Böhning-Gaese, Dumbo & Farwig 2010; Laurance, Nascimento, Laurance, Andrade, Fearnside et al. 2006). Moreover, forest relicts are often characterized by new abiotic conditions (e.g. altered irradiance, temperature regime or soil moisture), and biotic conditions (e.g. herbivory, seed dispersal or pollination) (Cadenasso & Pickett 2000). Two types of colonization can be defined, depending on the origin of the species. The colonization by a species present in the regional species pool, can be defined as an autochthonous species colonization (Fig. 1-2a), while the colonization by a species absent in the regional species pool (e.g. invasion by an exotic species or the colonization by a new species as an effect of changed climatic conditions) can be defined as an allochtonous species colonization (Fig. 1-2b). The number of species only present in the regeneration layer may complement the future tree layer composition and can therefore be defined as recruitment credit. For instance, the number of species absent from the mature tree layer but persistent in a seedling bank can be considered a recruitment credit. These tree seedlings or saplings can spend decades in the forest understory waiting for openings in the canopy to provide adequate light for growth in the canopy layer (Comita, Aguilar, Perez, Lao & Hubbell 2007; Comita & Hubbell 2009; Cruz-Rodriguez & Lopez-Mata 2004). The recruitment of seedlings and saplings to the life stage of mature trees depends on multiple stochastic, natural and anthropogenic factors and can result in successful (Fig. 1-3a) and unsuccessful (Fig. 1-3b) species recruitment. The quantification of the regenerating pool is a valuable indicator of potential future tree species composition, and possibly a counterbalancing addition to the extinction debt (Benítez-Malvido et al. 2003; Hylander & Ehrlén 2013; Kirika et al. 2010).

Vegetation change can directly be detected by repeated observation of permanent plots or simulation models can be used to forecast community dynamics (Feeley & Silman 2009; Hubbell, He, Condit, Borda-de-Agua, Kellner et al. 2008; Wearn, Reuman & Ewers 2012). However, such data is often not available for tropical regions and expertise is often lacking to run sophisticated models (Jackson et al. 2010). These approaches are often applied to determine extinction events, yet studies on both extinction and colonization events are scarce, especially in tropical regions (Comita et al. 2007; Jackson et al. 2010; Kirika et al. 2010; Metzger et al. 2009; Wearn et al. 2012). We developed and implemented a regional and a local species accounting equation, which allow the evaluation of the current forest composition and the assessment of potential future dynamics. For instance, the equation includes the quantification of potential extinction debt, colonization credit and recruitment credit. The surveys of mature tree, sapling and seedling layer composition were conducted in 82 plots localised in two relatively large, one medium sized and nine very small forest relicts in Taita Hills, Kenya. A simultaneous ordination of these datasets delivered insights in community composition dynamics due to potential species extinction, colonization or recruitment. More specifically we tested the following hypotheses:

(i) Tree species composition differs between life stages, both in large and small forest relicts.

(ii) The larger forest relicts are characterized by a low potential extinction debt, recruitment and colonization credit.

(iii) Small forest relicts have a high potential extinction debt and colonization credit and a low potential recruitment credit.

Materials and methods

Study area

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

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

Data collection

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

Species community composition change

At landscape level, a multiresponse permutation procedure (MRPP) test was used for testing the hypothesis of no difference between the three life stages and between the large and small forest relicts. The test statistic A is given as a descriptor of within group homogeneity, compared to random expectation. (McCune & Mefford 2002). Nonmetric multidimensional scaling (NMDS) (McCune & Mefford 1999) was used to assess the indirect gradients influencing the overall species composition changes at the several forest relicts for the three life stages (seedling, sapling and mature tree). The ordination was run on the presence-absence dataset using the Sørensen distance measure, six starting dimensions, 40 iterations and an instability criterion of 10^{-5} (McCune et al. 2002). Species scores were calculated with weighted averaging. Wilcoxon rank-sum test was used for the pairwise comparison of the length and the Rayleigh test for the direction of species composition shifts from seedling and sapling to mature tree layer.

Species accounting equations

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

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

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

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

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

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

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

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

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

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

Results

Tree species composition changes

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

Solving the species accounting equations

The values for the variables in the regional species accounting equation ($N_R = R + D_E + C_R + C_C$) were calculated based on the inventory of 82 plots. The regional species pool N_R was 78 species comprising 71 regenerating species R, seven species facing potential extinction (= extinction debt D_E) and no potential recruitment credit C_R. Assuming an allochtonous species colonization of zero (Fig. 1-2b; no invasion of exotic species or colonization by new species), the potential colonization credit C_C was set to zero as, per definition, the autochtonous colonization on regional level is always zero.

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

Discussion

Extinction and recruitment at landscape level

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

Species composition in forest relicts

As observed in other tropical forests (Farwig et al. 2008; Hill et al. 2001; Laurance et al. 2006; Lawes et al. 2007), several early-successional species dominate the mature tree layer of the smallest relicts. The large-scale logging of valuable timber trees (e.g. *Ocotea usambarensis* and *Podocarpus latifolius*) in the past and the large-scale conversion of indigenous forest to farmland have created gaps and edges, in which were subsequently colonized by light-demanding (e.g. *A. gummifera* and *Macaranga capensis*), disturbance-tolerant (e.g. *Tabernaemontana stapfiana*) or edge-associated species (*Maesa lanceolata*) (Comita et al. 2007; Kirika et al. 2010). Bussmann (2001) found similar successional trajectories and regeneration patterns for other montane forests of Kenya (e.g. Mount Kenya, Mt Nyiru) and Ethiopia (e.g. Menagesha forest). Conversely, the large relicts still harbor a large portion of late-successional species, most likely because natural regeneration of these species was less disturbed.

Dynamics in forest relicts

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

Species accounting equation performance

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

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

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

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

Conservation of forest relicts

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

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Appendix A. Supplementary data

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

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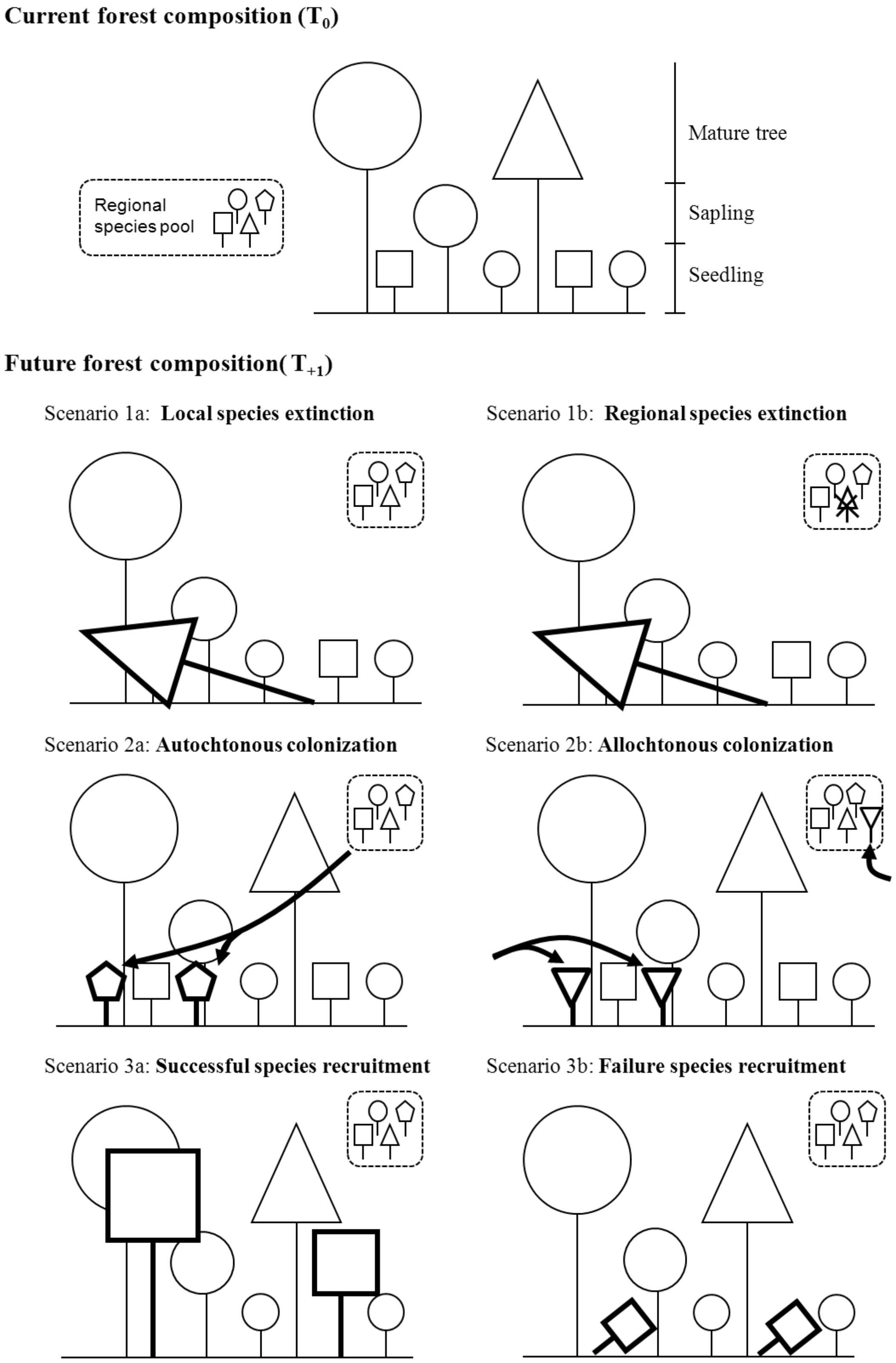
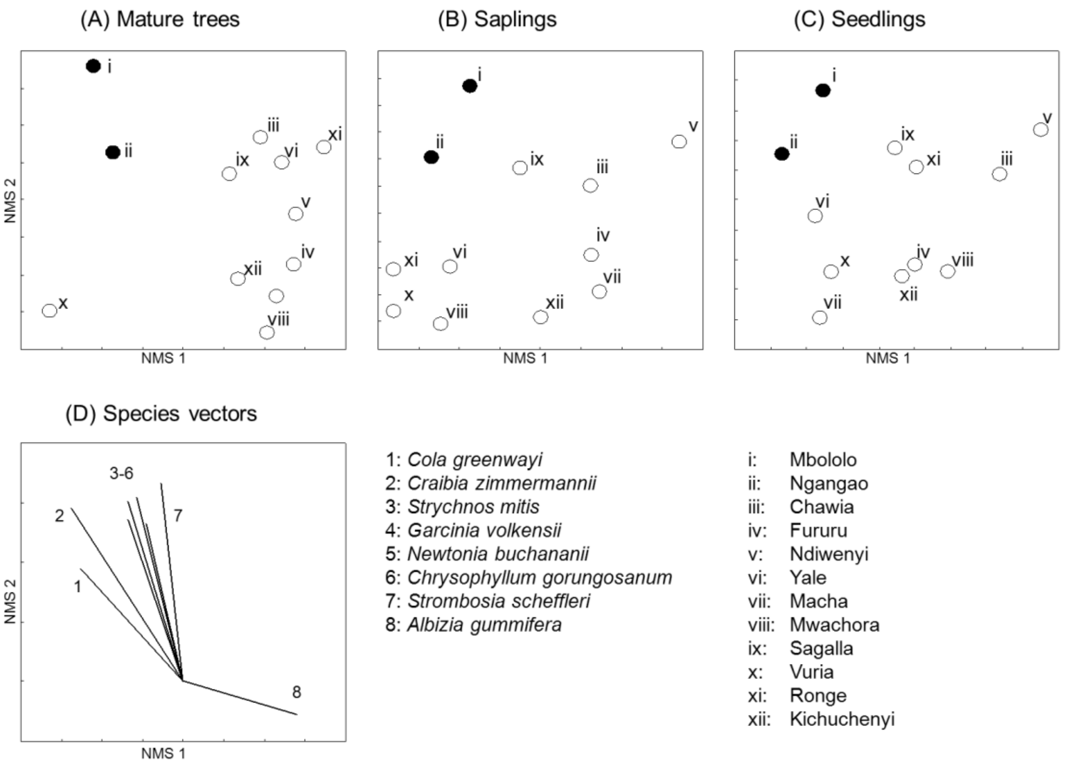
Figure legends

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

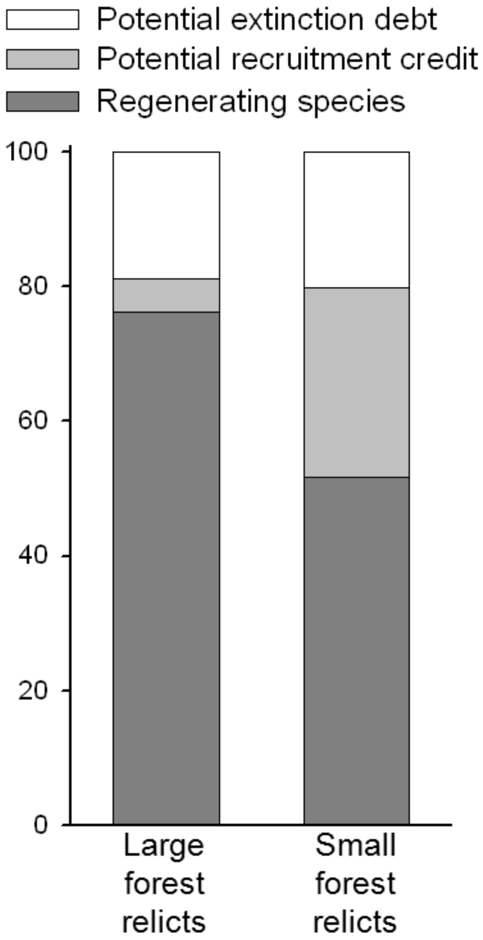
Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of the plot data (246 records = 82 plots × 3 life stages per plot) from 12 forest relicts in the Taita Hills, Kenya. NMDS ordination was performed simultaneously for three life stages but results are presented separately for mature trees (A),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

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

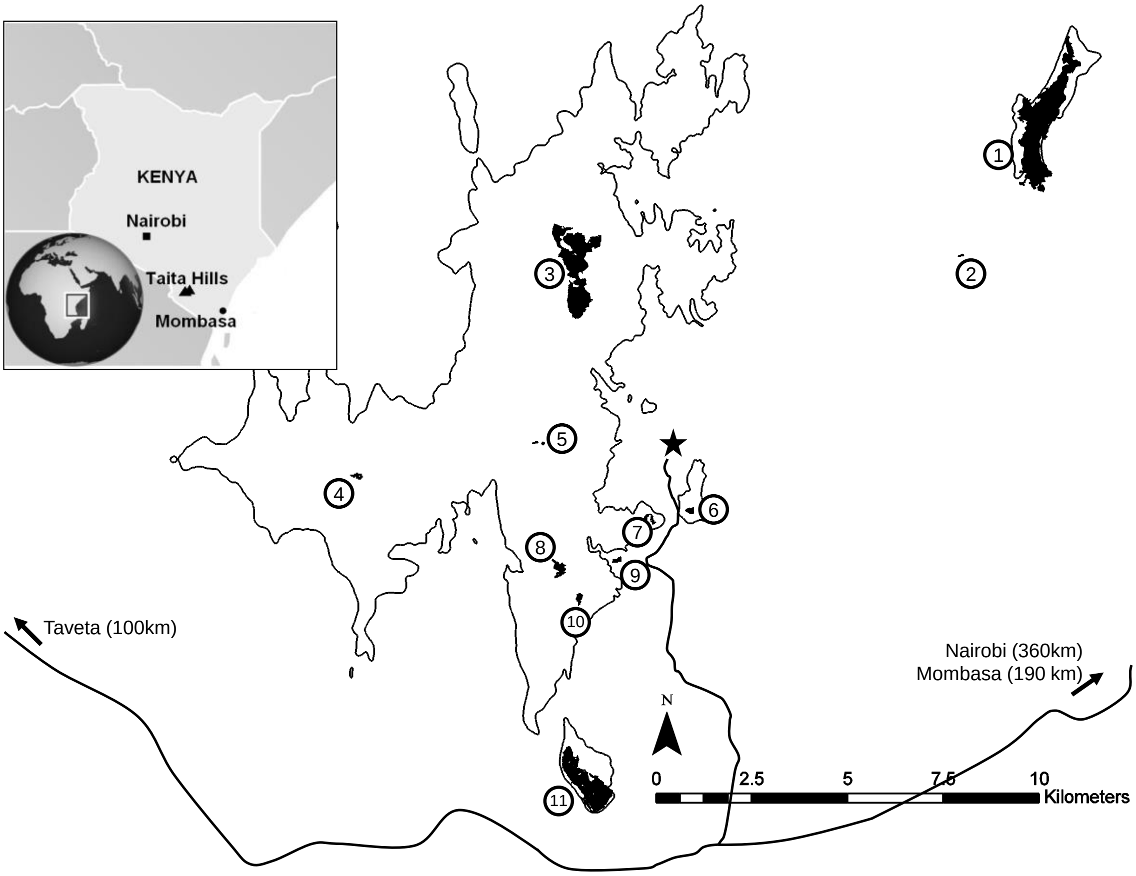

Current forest composition (T_0)
Regional species pool
Mature tree
Sapling
Seedling
Future forest composition(T_{+1})
Scenario 1a: Local species extinction
Scenario 1b: Regional species extinction
Scenario 2a: Autochtonous colonization
Scenario 2b: Allochtonous colonization
Scenario 3a: Successful species recruitment
Scenario 3b: Failure species recruitment



(A) Mature trees
(B) Saplings
(C) Seedlings
NMS 1
NMS 2
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
(D) Species vectors
1
2
3-6
7
8
1: *Cola greenwayi*
2: *Craibia zimmermannii*
3: *Strychnos mitis*
4: *Garcinia volkensii*
5: *Newtonia buchananii*
6: *Chrysophyllum gorungosanum*
7: *Strombosia scheffleri*
8: *Albizia gummifera*
i: Mbololo
ii: Ngangao
iii: Chawia
iv: Fururu
v: Ndiwenyi
vi: Yale
vii: Macha
viii: Mwachora
ix: Sagalla
x: Vuria
xi: Ronge
xii: Kichuchenyi


Potential extinction debt
Potential recruitment credit
Regenerating species
100
80
60
40
20
0
Large forest relicts
Small forest relicts

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



Appendix A: Table 1. Relevant information of the 12 indigenous forest relicts of Taita 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 *Saintpaulia teitensis* B.L.Burtt
Ngangao	120	17	1750-1900	03°21'S 38°20'E	Located on an eastern slope of a north-sou indigenous forest mixed with plantation fo surrounded by agricultural land and only l *Meineckia ovata* E.A. Bruce
Chawia	86	14	1500-1600	03°28'S 38°20'E	Southernmost, heavily disturbed forest lo gentle slopes; plantations of exotic trees i by agricultural land
Fururu	8	5	1650-1750	03°25'S 38°20'E	Partly disturbed forest relict with patches small remnant in the east and one in the s
Ndiwenyi	3	2	1600	03°26'S 38°20'E	Heavily disturbed forest relict and surrou
Yale	2	2	1850	03°24'S 38°20'E	Two small forest relicts; located on the ea oriented mountain ridge with very steep s with plantations.
Macha	2	2	1600	03°25'S 38°21'E	Located on a west-east oriented ridge; dis plantation and agricultural land
Mwachora	2	2	1650	03°25'S 38°22'E	East of Macha; located on steep hilltop; d agricultural land
Sagalla	2	2	1450-1500	03°30'S 38°35'E	Narrow strip of forest which receives mo than the other forest relicts; surrounded b the isolated Mount Sagalla, 25 km to the s relicts
Vuria	1	2	2200	03°24'S 38°17'E	Highest peak (2208m) and the westernmo small forest relict of closed canopy forest environment is heavily disturbed and has

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

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

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

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

1) Eastern Arc Mountain endemic species

2) Taita Hills endemic species

3) Late-successional species which we found in the regeneration layer of the small forest relicts. All these species are strongly affiliated with the large, intact forest relicts