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Relationships between the density of two potential restoration tree species and plant species abundance and richness in a degraded Afromontane forest of Kenya

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Abstract

In recent years, there have been considerable efforts to restore degraded tropical montane forests through active restoration using indigenous tree species. However, little is known about how these species used for restoration influence other species. In this study, two potential restoration species, *Albizia gummifera* and *Neoboutonia macrocalyx*, are investigated with regard to the relationship between their density and the abundance and richness of other plant species. The study was conducted in a degraded forest consisting of disturbed transition zones and secondary forest. Our results show positive relationships between the density of *A. gummifera* and the abundance of tree seedling and sapling richness in the transition zones and in the secondary forest. Shrub richness was negatively related to the density of *A. gummifera*. Abundance and richness of tree saplings and shrubs were positively related to *N. macrocalyx* density both in the transition zones and in the secondary forest. Herb species richness declined with *N. macrocalyx* density in the transition zones but increased with *N. macrocalyx* density in the secondary forest. The positive relationships between the density of the two tree species and species richness of other woody species suggest that both *A. gummifera* and *N. macrocalyx* can be suitable for active restoration of degraded mountain forests within their natural range.

Key words: Albizia gummifera, facilitation, forest restoration, *Neoboutonia macrocalyx*, pioneer species, species interactions

Résumé

Ces dernières années, il y a eu des efforts considérables pour restaurer des habitats montagnards tropicaux dégradés grâce à une restauration active utilisant des espèces d'arbres indigènes. Mais on sait peu de chose de la manière dont les espèces utilisées dans ce cadre influencent d'autres espèces. Dans cette étude, deux espèces potentielles pour une restauration *Albizia gummifera* et *Neoboutonia macrocalyx* sont étudiées pour la relation entre leur densité et l'abondance et la richesse d'autres espèces végétales. L'étude fut menée dans une forêt dégradée composée de zones de transition perturbées et de forêt secondaire. Nos résultats montrent des relations positives entre la densité d'*A. gummifera* et l'abondance de jeunes plants d'arbres et la richesse en jeunes arbres dans les zones de transition et la forêt secondaire. La richesse en arbustes était liée négativement à la densité d'*A. gummifera*. L'abondance et la richesse de jeunes arbres et d'arbustes étaient positivement liées à la densité de *N. macrocalyx* dans les zones de transition et dans la forêt secondaire. La richesse en espèces herbacées déclinait avec la densité de *N. macrocalyx* dans les zones de transition, mais augmentait avec elle dans la forêt secondaire. La relation positive entre la densité des deux espèces d'arbres et la richesse en espèces d'autres espèces ligneuses suggère qu'aussi bien *A. gummifera* que *N. macrocalyx* pourraient être bénéfiques pour une restauration active de forêts de montagne dégradées de leur aire de répartition naturelle.

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Introduction

The restoration of degraded tropical natural forests is receiving increasing attention (Parrotta, Turnbull & Jones, 1997; Kebrom & Tesfaye, 2000; Guariguata & Ostertag, 2001; Duncan & Chapman, 2003; Teketay, 2005; Aynekulu, Denich & Tsegaye, 2009). Because of a dramatic reduction in forest cover (FAO, 2009), drought due to climate changes (Millar, Stephenson & Stephens, 2007), the scarcity of forest products (FAO, 2009) and increased pressure on remnant natural forests, large areas of natural forests remain in a highly degraded state. It is increasingly recognized that traditional restoration methods, in particular monoculture plantations of exotic species, may be inappropriate because it does not contribute to restoration of biodiversity (Evans & Turnbull, 2004) and ecosystem functions (Wormald, 1992). Thus, the transformation of abandoned forest fallows into a regenerating forest rather than monoculture plantation of exotic species is a better way to achieve the ecological values from forest ecosystem (Shono, Cadaweng & Durst, 2007).

The most obvious change after disturbances in natural forests is the rapid emergence of pioneer plant species (Brokaw, 1987; Nykvist, 1996; Guariguata & Ostertag, 2001; Slik & Eichhorn, 2003). On severely disturbed forests, fast-growing pioneer tree species may both facilitate and inhibit recruitment of forest species during later successional phases (Kigomo, 1987; Teketay, 2005; Piotto, 2008). Facilitation, whereby the presence of one plant species enhances the establishment and survival of other plant species, is most often documented in stressful environments, such as arid, saline or cold ecosystems (Smit, Gusberti & Muller-Schaer, 2006). In such environments, the presence of a stress-tolerant facilitator can ameliorate the environmental conditions in its immediate vicinity through provision of shade or soil nutrients. Through such positive interactions, facilitators can strongly influence plant community composition and richness (e.g. Bertness & Callaway, 1994; Smit & Olff, 1998; Brooker *et al.*, 2008). However, other previous studies indicate that on severely degraded land, fast-growing pioneer tree species can prevent, or slow down, the colonization of other species (e.g. Bertness & Callaway, 1994; Chapman & Chapman, 1999) because of competition for resources and thus reduce the speed of forest succession (Berkowitz, Canham & Kelly, 1995) and also potentially change the direction of succession (Shono, Cadaweng & Durst, 2007). Thus, knowledge about how pioneer species affect the establishment, abundance and species richness of later successional species is highly relevant for successful active restoration. Indeed, several authors have warned against the use of species whose effects on other species are unknown (Wormald, 1992; Carnevale & Montagnini, 2002; Montagnini, Ugalde & Navarro, 2003).

In Kenya, large areas of natural forests have been heavily disturbed through selective logging and clearing since colonial times (1930s) to 1986, after which logging was banned (MENR, unpublished data). The degraded areas form mosaics that comprise a range of habitat types, such as pastures, old plantations and abandoned fallows left to succession. In the Mau Forest, the area of this study, degraded areas are going through a recovery process whereby competition and facilitation possibly occur simultaneously during succession towards secondary forest. Exotic species have been planted to restore such degraded forest systems in the tropics, including Kenya, but this has mainly contributed to the creation of monocultures that decrease ecosystem function and biodiversity (Evans & Turnbull, 2004). In Kenya, active restoration of degraded forest areas has been initiated by planting a mixture of indigenous pioneer and nonpioneer tree species (GOK, 2005; KEFRI, unpublished data). However, most of these species' ecological and silvicultural requirements are not known. Overall, there is lack of information to guide the selection of restoration species for degraded forests. Importantly, this information should include not only the ecological requirements of restoration species, but also how they potentially affect other species during succession, the focus of this study.

Mullah, Totland & Klanderud (2011) in a study of the abundance, richness and composition of regenerating forests along a disturbance gradient from abandoned fallows and into the secondary forest found that *Albizia gummifera* (J.F.Gmel.) and *Neoboutonia macrocalyx* (Pax) occurred in all life stages both in regenerating forest and in the secondary forest. This suggests that the two species may be good candidates for active restoration because they have the ability to establish as seedlings and survive as saplings in sites with different degrees of degradation. However, their potential influences on other species are not known, even though *A. gummifera* is already promoted as a multipurpose species that can be used in active restoration (Bertness & Callaway, 1994; Bristow *et al.*, 2007). We postulate that both species may facilitate the succession in the transition zones. The two tree species may also positively influence the abundance and richness of other plant species associated with them both in transition zones and in the secondary forest.

In this study, we examined the relationship between the density of these two tree species and the abundance and richness of the rest of the plant community, to examine their suitability for active restoration. In particular, we ask the following questions: (i) Is there a relationship between the density of *A. gummifera* and *N. macrocalyx* and the abundance and richness of seedlings and saplings of other tree species, shrubs, lianas and herbs in disturbed transition zones and in the secondary forest? (ii) How do the densities of the two species relate to each other in disturbed transition zones and in the secondary forest? and (iii) What is the relationship between the density of the two species and the composition of other tree seedling and sapling species in the transition zones and in the secondary forest?

Material and methods

Study area

Mau Forest is the largest remaining near-continuous montane indigenous forest in East Africa. It is composed of natural primary forests, swamps, grasslands, fallows and regenerating forests. The study area is at 2120 m altitude with an annual rainfall around 2000 mm. Mean annual temperature ranges from 12 to 16°C, and potential evapotranspiration varies between 1400 and 1800 mm (Jackson & McCarter, 1994). The natural forest consists of Afromontane bamboo at the higher altitudes and secondary plant communities derived from logged rainforest at lower altitudes. The forest has a high biodiversity and hosts indigenous tree species, such as *Olea europeae ssp africana* (P.S.Green) and *Dombeya goetzenii* (Bamps.), and Yushania *alpina* (K.Schum.) (MENR, unpublished data; Kinyanjui, 2009). Within Itare forest block, 15 ha of previously cleared, cultivated and then abandoned area (19 years ago), surrounded by secondary forest, was chosen for this study. The study site consisted of zones of different degrees of disturbance, with the most degraded zone dominated by early colonizing shrubs and a few tree seedlings, here termed 'transition zone one' (TZI), and a less degraded zone consisting of shrubs and seedlings, saplings and adult trees, termed 'transition zone two' (TZII). The transition zones were surrounded by a secondary forest consisting of secondary plant communities derived from artisanal (pit sawing) logged rainforest. For more details about the study area, readers are referred to the study of Mullah, Totland & Klanderud (2011).

Study species

In a previous study, Mullah, Totland & Klanderud (2011) found seven indigenous tree species, *Polyscias fulva* (Harms), *Psychotria mahonii* (C.H.Wright), *Allophylus abyssinicus* (P.Beauv.), *Albizia gummifera* (J.F.Gmel.), *Neoboutonia macrocalyx* (Pax.), *Dombeya torrida* (Bamps.) and *Ekebergia capensis* (Sparm.), to be abundant and present in all life stages in both the disturbed transition zones and in the secondary forest in the study area. All these tree species could be good candidates as restoration species because of their ability to establish as seedlings in heavily disturbed sites and to survive as saplings and adults under different conditions in the area. In this study, we focus on *A. gummifera* and *N. macrocalyx* because they had abundances (160 and 89 individuals/ha, respectively, in transition zones, and 524 and 354 individuals/ha, respectively, in the secondary forest) that allowed sound statistical assessments of their relationships with other species. Both of these species are regarded as pioneers of moist (Beentje, 1994) and secondary forest (Bussmann, 1999; Chapman *et al.*, 1999).

Albizia gummifera is a medium-to-large deciduous tree, 15–30 m tall, native to African montane moist forests, and classified as a forest edge species (Beentje, 1994). The regeneration status of the species is poorly known, but seeds are dispersed by wind, which significantly increases its colonization success (Noad & Birnie, 1990). *A. gummifera* is dinitrogen fixing and increases soil nitrogen content and thus enhances nitrogen transfer to associated nonfixing species during natural succession (Raquena *et al.*, 2001; Odee *et al.*, 2002). Dinitrogen-fixing species may be key components of the natural succession in semi-arid ecosystems (Kadiata, Mulongoy & Isirimah, 1996). Furthermore, a growing number of studies report successful utilization of *A. gummifera* as a facilitator in agroforestry systems (Palmer & Pitman, 1972; Aerts *et al.* 2007 (Teklay & Malmer, 2004).

Neoboutonia macrocalyx is an indigenous tree of upland natural forest, 10–20 m high – a fast-growing pioneer species abundant in montane forests that have been heavily disturbed or cleared (Beentje, 1994; Katende, Birnie & Tengnas, 1995). It coppices well, and the seeds are dispersed by animals (Chapman *et al.*, 1999). As far as we know, there have not been any previous studies on *N. macrocalyx* and its relationship with other plants in any forest ecosystem.

Data collection

We collected data in November 2006 in the middle of the dry season and in March 2007 at the beginning of the rainy season. We randomly selected 34 plots as follows: twenty plots in the disturbed transition zones (TZ) and fourteen plots in the secondary forest (SF). We counted individuals of *A. gummifera*, *N. macrocalyx* and all other woody species and estimated percentage cover of herbaceous species in all the plots. We used plots of 5 × 30 m in TZI and 10 × 30 m in TZII and SF. Each plot was divided into six subplots (for the 5 × 30 m plots) and 12 subplots (for the 10 × 30 m plots), and each subplot had a 1 × 1 m quadrat in its centre. Adult trees and lianas (taller than 1.3 m and diameter at breast height (dbh) >10 cm) were counted in all subplots. Tree saplings (young trees taller than 1.3 m and dbh <10 cm) and shrubs were counted in every other subplot. Tree seedlings (<1.3 m height) and herbs were recorded in a central quadrat within each subplot. We used larger plots in TZII and SF to capture the variation in tree species richness, abundance and composition in these zones. To enable comparison between the different plot sizes, corrections were made before data analyses. For the species abundance data, we divided abundance within 10 × 30 m plots by two. For the species richness data, we calculated the mean number of species within each of the two 5 × 30 m plots and used the mean of these in the analyses. Nomenclature follows Agnew and Agnew (1994) and Beentje (1994).

Statistical analyses

We used simple linear regressions to examine the relationships between *A. gummifera* and *N. macrocalyx* density and the abundance and richness of other plant species. In the analysis, we used the sum of adults and saplings (for sound statistical analyses) to represent the density of *A. gummifera* and *N. macrocalyx* as independent variables. To control for the difference in plots sizes used in our study, we computed 'true' richness by Mao Tao estimator using the software EstimatesS, version 8.2.0 (Colwell, 2009), and used R 2.10.0 software (R-Development Core Team, 2009) to produce the species accumulation curves for each life form and zone. Mean abundance and 'true' species richness of seedlings and saplings of other tree species, shrubs, lianas and percentage cover of herbs were used as dependent variables in separate regression analyses. We also performed a correlation analysis to examine the extent to which the two species are associated. We conducted separate analyses for plots in the transition zones (transition zones I and II combined) and in the secondary forest. The abundance and richness values were log-transformed prior to the analyses. SYSTAT 10 for windows was used for the regression analyses.

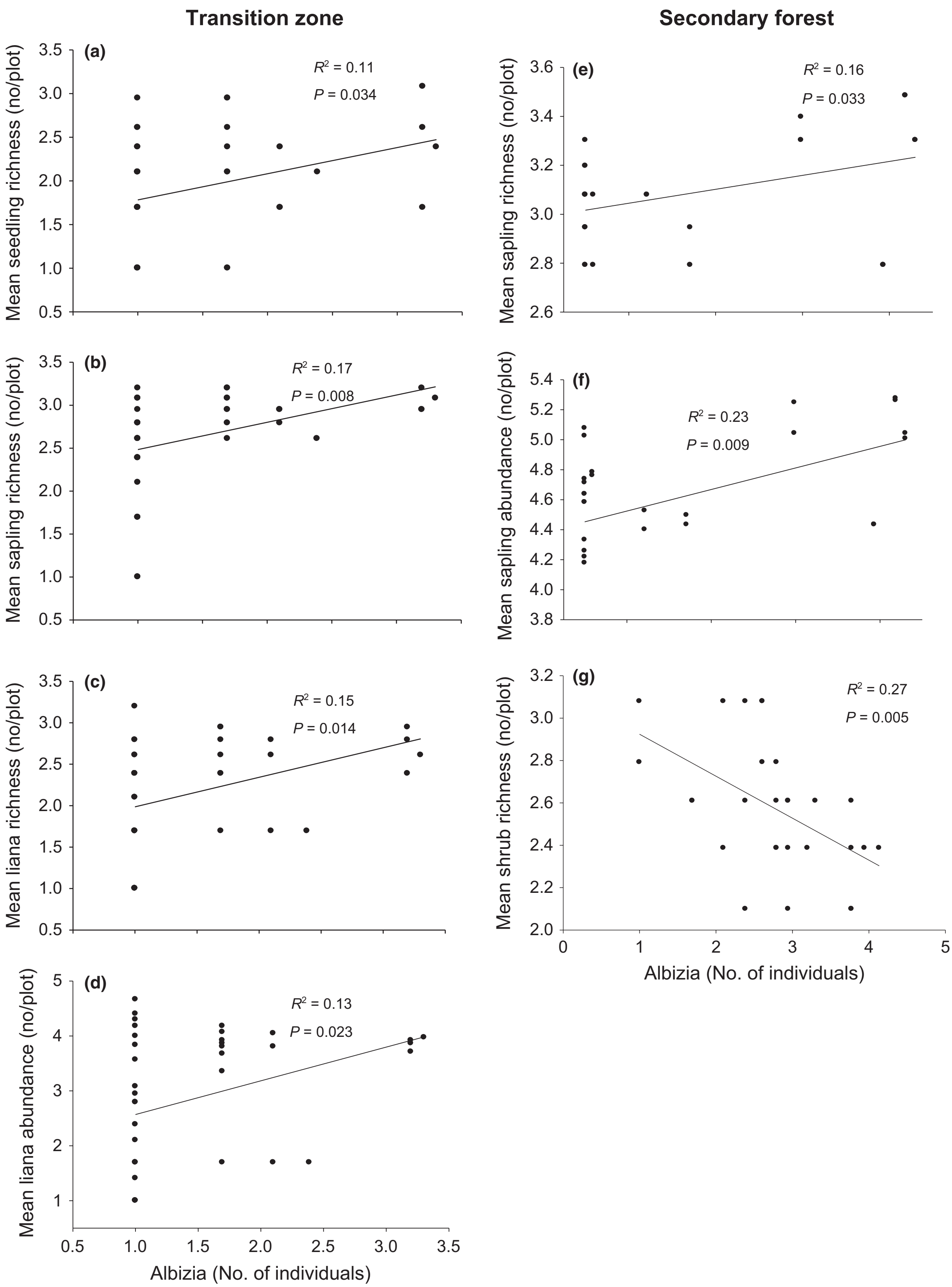
We used multivariate ordination analyses to examine how the two potential restoration tree species contributed in explaining species composition of other tree seedling and sapling species in the transition zones and in the secondary forest, and how other tree species were associated with *A. gummifera* and *N. macrocalyx*. The density of *A. gummifera* and *N. macrocalyx* was used as environmental variables in a canonical correspondence analysis (CCA), and their relationship with the species composition was tested by forward selection using 999 permutations. We did separate analyses for the transition zones, for the secondary forest and for tree seedling and sapling species composition. We tested for the significance of all canonical axes together, with 999 unrestricted permutations in a Monte Carlo test. All the ordinations were carried out using default settings in CANOCO 4.5 and graphs produced in CanoDraw (Ter Braak & Smilauer, 2002).

Results

Relationships between other species and the density of A. gummifera *and* N. macrocalyx

Simple regressions showed that there was a positive relationship between species richness of seedlings and saplings of other tree species and the density of *A. gummifera* in the transition zones (Fig. 1a,b). Species richness and

Fig 1 Relationship between *Albizia gummifera* density and (a) tree seedling richness, (b) tree sapling richness, (c) liana richness, and (d) mean liana abundance in the transition zones and (e) tree sapling richness, (f) mean tree sapling abundance, (g) mean herb abundance, and (h) shrub richness in the secondary forest in Mau Forest, Kenya


Transition zone
Secondary forest
(a)
R^2 = 0.11
P = 0.034
Mean seedling richness (no/plot)
(b)
R^2 = 0.17
P = 0.008
Mean sapling richness (no/plot)
(c)
R^2 = 0.15
P = 0.014
Mean liana richness (no/plot)
(d)
R^2 = 0.13
P = 0.023
Mean liana abundance (no/plot)
Albizia (No. of individuals)
(e)
R^2 = 0.16
P = 0.033
Mean sapling richness (no/plot)
(f)
R^2 = 0.23
P = 0.009
Mean sapling abundance (no/plot)
(g)
R^2 = 0.27
P = 0.005
Mean shrub richness (no/plot)
Albizia (No. of individuals)

abundance of lianas were also positively related to *A. gummifera* density (Fig. 1c,d), whereas the abundance of seedlings and saplings of other tree species, shrubs and herbs was not related to *A. gummifera* density in the transition zones In the secondary forest, tree sapling species richness and abundance were positively related to *A. gummifera* density (Fig. 1e,f), whereas shrub richness was negatively related to *A. gummifera* density (Fig. 1g). There were no significant relationships between species richness and abundance of tree seedlings, lianas and shrub abundance, or herb cover with *A. gummifera* density in the secondary forest.

In the transition zones, there was a positive relationship between the abundance of tree saplings and *N. macrocalyx* density (Fig. 2a), whereas herb species richness was negatively related to *N. macrocalyx* (Fig. 2b). Mean species abundance and richness of tree seedlings, species richness of saplings, shrubs and lianas were not related to *N. macrocalyx* density in the transition zones. In the secondary forest, the species abundance and richness of tree saplings and species richness of shrubs and herbs were positively related to *N. macrocalyx* density (Figs. 2c–f). Mean species abundance and richness of tree seedlings and lianas, and the abundance of shrubs and herb cover were not related to *N. macrocalyx* density in the secondary forest.

Relationship between A. gummifera *and* N. macrocalyx

There was a positive correlation between the abundance of *N. macrocalyx* seedlings and *A. gummifera* adults, whereas *N. macrocalyx* seedlings, saplings and adults were positively correlated with *A. gummifera* seedlings in the transition zones (Table 1). There was no significant correlation between *N. macrocalyx* seedlings, saplings and adults and *A. gummifera* saplings in the transition zone (Table 1). Mean abundance of *N. macrocalyx* saplings was negatively correlated with *A. gummifera* saplings density in the secondary forest (Table 1).

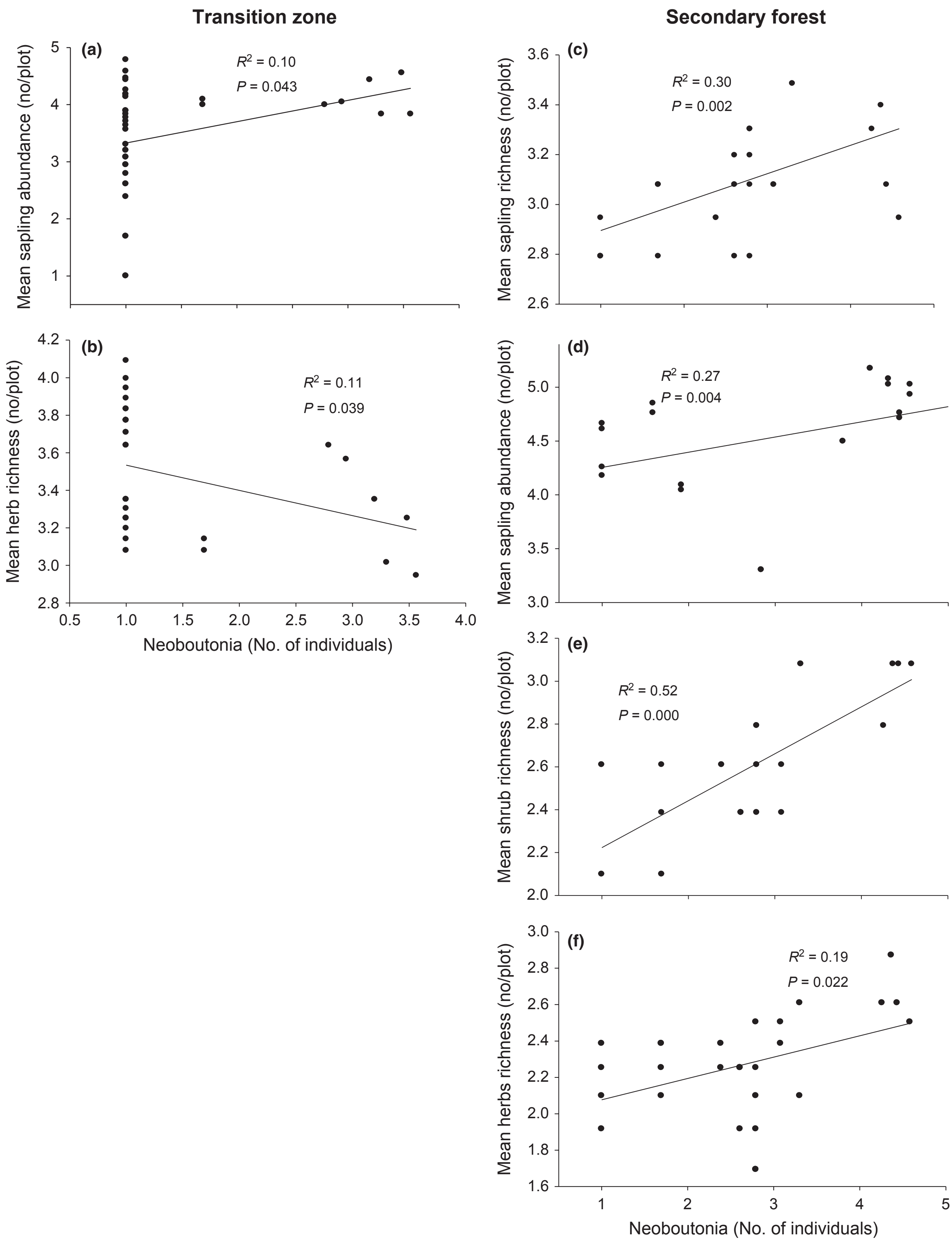
Relationship between species composition and the abundance of A. gummifera *and* N. macrocalyx

The CCA model was significant for tree saplings ($F = 2.45$, $P < 0.01$), but not for seedlings ($F = 1.19$, $P = 0.292$) in the transition zones (Fig. 3a,b), and for seedlings ($F = 3.50$, $P < 0.01$) and saplings ($F = 7.85$, $P < 0.001$) in the secondary forest (Fig. 3c,d). In the transition zones, saplings of shade-intolerant pioneer species, for instance, *Hagenia abyssinica* (J.F.Gmel.), *A. abyssinicus*, *Macaranga kilimandscharica* (Pax) and *Dovyalis macrocalyx* (Oliv.), were positively associated with *A. gummifera*, whereas saplings of some forest interior (shade-tolerant) species like *Tabernaemontana stapfiana* (Brittene) and *Polyscias fulva* (Hiern) were more related to *N. macrocalyx* (Fig. 3b). In the secondary forest, seedlings and saplings of *Garcinia buchananii* (Baker), *Syzygium guineense* (F.White), *Casearia battiscombei* (R.E.Fr.) and *T. stapfiana*, most of which are forest interior species, were associated with *A. gummifera* (Fig. 3c,d). Seedlings of *Prunus africana* (Hook.f.), *P. fulva*, *Celtis gomphophylla* (Baker) *and A. abyssinicus*, which are shade-intolerant species, and saplings of *P. africana*, *D. torrida*, *Zanthoxylum gillettii* (Engl.), *Croton macrostachyus* (Hochst.ex Delile), *P. fulva* and *Ehretia cymosa* (Brenan) were associated with *N. macrocalyx* (Fig. 3c,d). *Polyscias fulva* was associated with *N. macrocalyx* both in the transition zones and in the secondary forest, both as seedlings and saplings (Fig. 3a–d).

Discussion

Our results of the potential role of *A. gummifera* and *N. macrocalyx* in the abundance of species and species richness suggest that these two species may primarily aid the establishment and abundance of other species and that they promote species richness during forest recovery. Tree seedlings and saplings in both the transition zones and in the secondary forest were positively related to *A. gummifera* density. Previous studies have found a strong influence of *A. gummifera* on associated plants due to its ability to fix nitrogen in different systems. For instance, strong influence of *A. gummifera* on associated plants in different agroforestry systems has been reported by Franco & de Faria (1997)and Gathumbi *et al.* (2002) who found that *A. gummifera* may aid forest regeneration through its positive effect on soil nitrogen. Various species of *Eucalyptus* also grow better when mixed with woody legumes, such as *Albizia* and *Acacia* (Binkley *et al.*, 1992; DeBell,

Fig 2 Relationship between *Neoboutonia macrocalyx* density and (a) mean tree sapling abundance and (b) herb richness in the transition zones, and (c) mean shrub abundance, (d) shrub richness, (e) herb richness, (f) tree sapling richness and (g) mean tree sapling abundance in the secondary forest in Mau Forest, Kenya


Transition zone
Secondary forest
(a)
R^2 = 0.10
P = 0.043
Mean sapling abundance (no/plot)
(b)
R^2 = 0.11
P = 0.039
Mean herb richness (no/plot)
Neoboutonia (No. of individuals)
(c)
R^2 = 0.30
P = 0.002
Mean sapling richness (no/plot)
(d)
R^2 = 0.27
P = 0.004
Mean sapling abundance (no/plot)
(e)
R^2 = 0.52
P = 0.000
Mean shrub richness (no/plot)
(f)
R^2 = 0.19
P = 0.022
Mean herbs richness (no/plot)
Neoboutonia (No. of individuals)

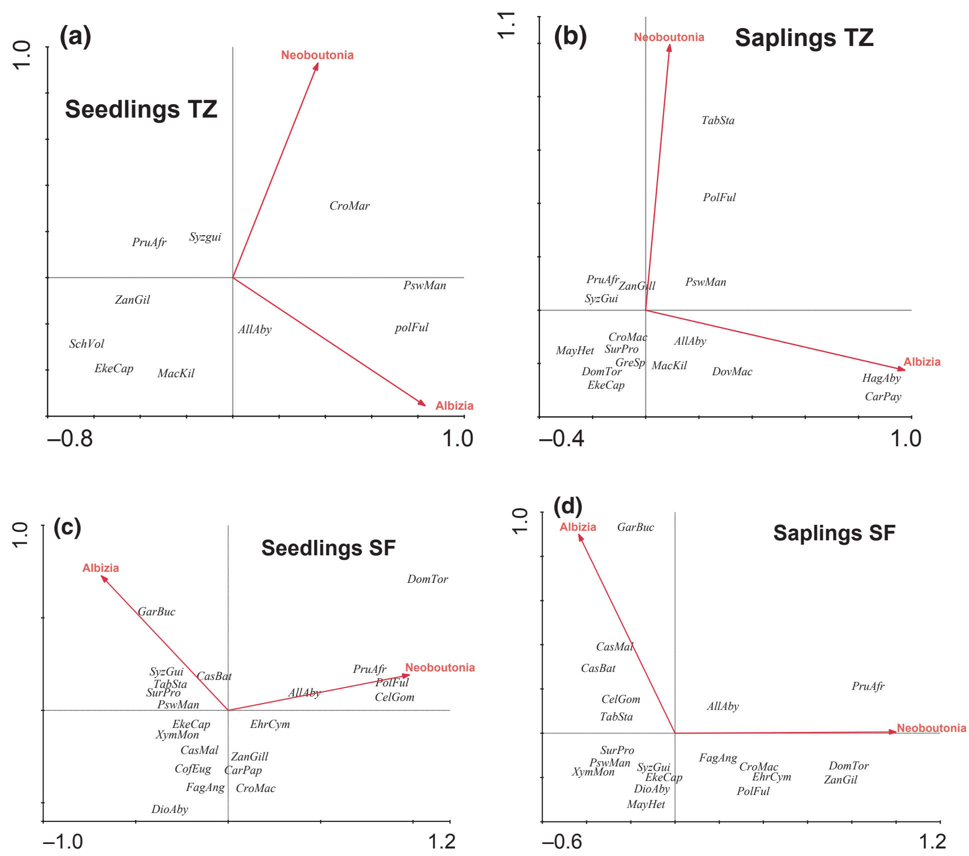


Fig 3 CCA plots of the relationships between the species composition of (a) tree seedlings in TZ, (b) tree saplings in TZ, (c) tree seedlings in SF, and (d) tree saplings in SF, and the density of *Albizia* and *Neoboutonia*. TZ, transition zone; SF, secondary forest; CroMac, *Croton macrostachyus;* CasBat, *Casearia battiscombei*; CasMal, *Cassipourea malosana*; AllAby, *Allophylus abyssinicus*; TabSta, *Tabernaemontana stapfiana*; XymMon, *Xymalos monospora*; SurPro, *Suregada procera*; EhrCym, *Ehretia cymosa*; GarBuc, *Garcinia buchananii*; CofEug, *Coffea eugenioides*; PsyMah, *Psychotria mahonii*; SyzGui, *Syzygium guineense*; EkeCap, *Ekebergia capensis*; PruAfr, *Prunus africana*; SchVol, *Schefflera volkensii*; CarPap, *Carica papaya*; FagAng, *Fagaropsis angolensis*; CelGom, *Celtis gomphophylla*; DioAby, *Diospyros abyssinica*; DomTor, *Dombeya torrida*; ZanGil, *Zanthoxylum gillettii*; PolFul, *Polyscias fulva*; MacKil, *Macaranga kilimandscharica*; MayHet, *Maytenus heterophylla*; GreSpp, *Grewia* species; HagAby, *Hagenia abyssinica*. Only well-fitting species are shown in the figure

Table 1 Results for correlation analysis between different growth forms of *Albizia gummifera* and *Neoboutonia macrocalyx* in the transition zones and in the secondary forest at Mau Forest, Kenya

	Albizia adults		*Albizia* saplings		*Albizia* seedlings	
	r	*P*	*r*	*P*	*r*	*P*
Transition zones						
Neoboutonia adult	**0.327**	**0.040**	−0.090	0.582	**0.471**	**0.002**
Neoboutonia saplings	0.238	0.139	−0.137	0.398	**0.374**	**0.017**
Neoboutonia seedlings	**0.309**	**0.052**	−0.055	0.738	**0.435**	**0.005**
Secondary forest						
Neoboutonia adult	−0.327	0.090	−0.103	0.603	−0.159	0.420
Neoboutonia saplings	−0.036	0.855	**−0.493**	**0.008**	−0.306	0.114
Neoboutonia seedlings	−0.168	0.392	−0.322	0.095	−0.077	0.698

Pearson's correlation coefficient and *P*-values are shown for each predictor; significant values ($P < 0.05$) are in bold.

Cole & Whitesell, 1997; Khanna, 1997; Bristow *et al.*, 2007). Furthermore, the symbiosis between *A. gummifera* and rhizobia has been shown to aid restoration of desertified ecosystems by providing 28–72% of the soil nitrogen through fixing of atmospheric nitrogen (Kadiata, Mulongoy & Isirimah, 1996). However, still considerably less is known about nitrogen fixation in tropical forest (Barron, Purves & Hedin, 2010). Results from lowland tropical forest also show that leguminous trees are only able to fix nitrogen in areas with history of disturbance and in the forest gaps (Sylvester-Brandley *et al.*, 1980; Saur *et al.*, 1998; Koponen *et al.*, 2003), conditions similar to our study site. This suggests that it is possible that *A. gummifera* is able to fix nitrogen in the transition zones in our site. This offers strong support for the idea that nitrogen-fixing legumes like *A. gummifera* have the ability to assist other plants in a naturally regenerating degraded abandoned fallow in the tropics. Thus, our results, and those of others, strongly suggest that *A. gummifera* can be used successfully in active restoration. *Neoboutonia macrocalyx* had a positive relationship with tree saplings abundance in both the transition zones and the secondary forest, suggesting that also this species may be used successfully in active restoration. *Neoboutonia macrocalyx* is not known to be nitrogen fixing, and it is likely that it promotes the establishment of others by provision of shade. Overall, both species were related to less light-tolerant tree species in both zones, which agrees with Richards (1996), who reported that pioneer species provide a canopy beneath which shade-tolerant species establish.

Albizia gummifera and *Neoboutonia macrocalyx* differed in their relationships with the other plants in both the transition zones and in the secondary forest. In the transition zones, *A. gummifera* was positively related to a higher number of growth forms than *N. macrocalyx*, suggesting that during changing succession conditions, *A. gummifera* might be a better facilitator than *N. macrocalyx*. The reason could be that *A. gummifera*, through its positive effect on soil nitrogen, aids the establishment of other plants as other studies suggest (Kadiata, Mulongoy & Isirimah, 1996; Teklay & Malmer, 2004; Bristow *et al.*, 2007). Positive relationship between the density of *A. gummifera* and *N. macrocalyx* in the transition zones suggests that they may have complementary effects on each other and could be used together in restoration in the same planting systems. However, in the secondary forest, due to limited space in the gaps where they occur, the two species seem to compete.

Our nonexperimental results suggest that *A. gummifera* and *N. macrocalyx* both assist and compete with other plant species. However, these patterns could also emerge through plant responses to other variables (e.g. soil nutrient availability, moisture) that affect the densities of *A. gummifera*, *N. macrocalyx* and other plant species. Simple correlative studies like ours are one way of practically assessing the suitability of species as restoration tools. It is beyond the scope of our study to draw additional conclusions about these other abiotic or ecological factors on the observed relationships. The emergence of these correlative relationships that support facilitation offers unique opportunity for further experimental studies to truly assess how these and other pioneer tree species interact with other plant species across ecosystems and disturbance types in the forest.

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