

Forest-fragment quality rather than matrix habitat shapes herbivory on tree recruits in South Africa

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Abstract: Forest fragmentation can alter herbivory on tree recruits with possible consequences for regeneration. We assessed effects of forest-fragment quality (tree diversity, vegetation complexity, relative abundance of pioneer trees) and matrix habitat on arthropods and herbivory in KwaZulu-Natal, South Africa. We compared arthropod abundances and herbivory on woody seedlings and saplings among four forest-fragment types differing in size and matrix (large fragments and small fragments surrounded by natural grassland, eucalypt and sugarcane plantations; $n_{\text{plots}} = 24$) using analyses of covariance. We recorded 3385 arthropods and inspected 897 seedlings (71 species) and 876 saplings (91 species). Relative abundance of predators increased with fragment quality; that of herbivores decreased. Herbivory responses to fragment quality varied: seedling herbivory decreased with relative abundance of pioneers and sapling herbivory increased with vegetation complexity. Matrix effects were low with little variation in relative abundance of predators (0.39–0.53) and herbivores (0.22–0.32), proportion of seedling (8.3–11.0%) and sapling herbivory (12.4–14.3%) among the forest-fragment types. These findings indicate that herbivory on tree recruits is mediated by forest-fragment quality rather than matrix habitat. Future studies should evaluate whether contrasting effects of fragment quality on arthropods and herbivory are caused by weak trophic interactions and variable herbivore compositions.

Key Words: arthropods, diversity–herbivory relationships, habitat quality, insects, KwaZulu-Natal, leaf damage, plant–animal interactions, saplings, scarp forest, seedlings

INTRODUCTION

Human activities, such as forest fragmentation and agricultural intensification, threaten biodiversity (Sala *et al.* 2000, Tylianakis *et al.* 2008). The consequences of this biodiversity decline for ecological processes are far from being understood (Balvanera *et al.* 2006). Accordingly, antagonistic interactions, like insect herbivory, might be subject to changes with potentially critical outcomes for forest regeneration.

Insect herbivory is the predominant form of leaf damage in (sub-)tropical forests (García-Guzmán & Dirzo 2001). Insect herbivory on woody seedlings and saplings may not only affect growth, productivity and survival of individual plants, but also alter the dynamics and structure of (sub-)tropical forests (Maron & Crone 2006).

Insect herbivory on woody seedlings and saplings has been shown to be affected by forest fragmentation (Ruiz-Guerra *et al.* 2010, Wirth *et al.* 2008). In a

recent review Wirth *et al.* (2008) identified three main factors at forest edges affecting herbivory, which should also be applicable to forest fragments: changes in (1) environmental conditions, (2) resource availability and quality and (3) trophic interactions. For instance, altered environmental conditions at forest edges lead to increased tree mortality in forest fragments (Laurance *et al.* 2001, 2006). Declined tree diversity might amplify insect herbivory in forest fragments as herbivory tends to be higher in less diverse and complex systems (Jactel & Brockerhoff 2007, McCann *et al.* 1998). Furthermore, the proliferation of light-demanding pioneer species at forest edges (Laurence *et al.* 2006) may alter resource availability and quality for herbivores in forest fragments. As pioneer trees are generally preferred by herbivores due to their higher nutritive value (Coley 1980), herbivory has been observed to be higher in pioneer-dominated forest stands (Richards & Coley 2007, Ruiz-Guerra *et al.* 2010).

Despite the evidence indicating that reduced forest-fragment quality should intensify insect herbivory

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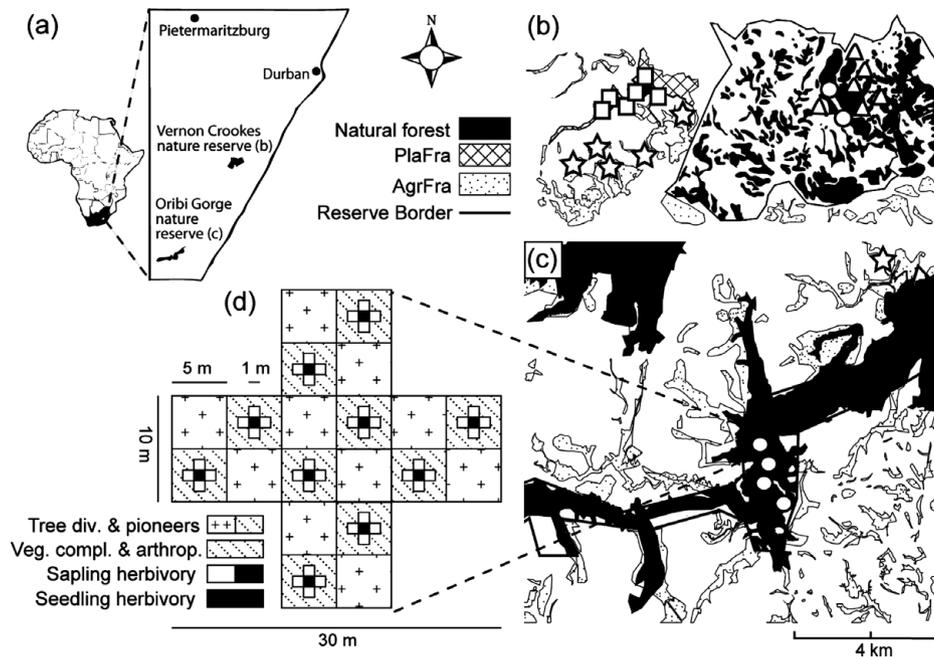


Figure 1. Map of study area in South Africa and schematic diagram of study plots. Enlarged study area in KwaZulu-Natal (a) with detailed maps of matrix landscapes around Vernon Crookes (b) and Oribi Gorge nature reserves (c) showing the 24 study plots (12 000 m²) with six each in large natural-forest fragments (ForFra; circles), small natural-forest fragments surrounded by grassland (GraFra; triangles), and in small modified-forest fragments surrounded by plantations (PlaFra; squares) and sugarcane agriculture (AgrFra; stars). Schematic diagram of 500-m² study plots (d) including subplots for assessing tree diversity (Tree div.), relative abundance of pioneer trees (pioneers), vegetation complexity (Veg. compl.), relative arthropod abundance (arthrop.) and seedling and sapling herbivory.

in forest fragments, many studies have found less herbivory or a neutral response to fragmentation (Benítez-Malvido & Lemus-Albor 2005, Ruiz-Guerra *et al.* 2010). Possibly, fragmentation limits herbivore dispersal (Faveri *et al.* 2008). Consequently, also the matrix landscape surrounding forest fragments may influence herbivory (Tscharrntke & Brandl 2004). Depending on permeability, matrices can complement natural habitat and facilitate dispersal of, for example, insectivorous predators or herbivores among habitat remnants (Faveri *et al.* 2008, Tscharrntke *et al.* 2005). However, matrices might also function as ecological traps for predators and release herbivores from top-down regulation in forest fragments (Terborgh *et al.* 2001).

Here we examined the effects of forest-fragment quality and matrix habitat on arthropod predators and herbivores as well as on insect herbivory on the natural woody seedling and sapling community in subtropical scarp-forest fragments in KwaZulu-Natal, South Africa. We determined the influence of forest-fragment quality in terms of tree diversity, vegetation complexity, and relative abundance of pioneer trees. We compared matrix effects across four forest-fragment types that were either surrounded by natural or by modified matrices. We expected (1) forest-fragment quality to increase predator abundance and decrease herbivore abundance as well as herbivory. We hypothesized (2) that natural matrix

habitat facilitates predator dispersal, which reduces herbivory in fragments with natural matrix habitat.

STUDY SITE

We collected our data from January to April 2010 in coastal scarp forest in KwaZulu-Natal (KZN), South Africa, within and close to Vernon Crookes (VC; 30°15'S–30°18'S, 30°32'E–30°37') and Oribi Gorge (OG; 30°41'S–30°45'S, 30°10'E–30°18.5'E) nature reserves (Figure 1a). Scarp forest forms a transition zone between Afromontane forest and Indian Ocean coastal-belt forest. It is located on the south- and south-east-facing slopes or in deep gorges (Eeley *et al.* 1999). These moist and sheltered microclimatic and topographic conditions have certainly contributed to the essential role of scarp forests as refugia during the last glacial maximum. Thus, scarp forests contain much of the region's biodiversity (Eeley *et al.* 1999, Lawes 1990). Most of the rainfall occurs between October and March and ranges from 440–1400 mm while the annual temperature ranges from 4 °C to 32 °C (Cooper 1985).

We studied four scarp-forest-fragment types that were either surrounded by natural matrices, i.e. large natural-forest fragments and small forest fragments surrounded by natural grassland or embedded in modified matrices,

i.e. eucalypt plantations or sugarcane agriculture (Figure 1b,c). In each of the four scarp-forest-fragment types we established six study plots of 500 m² resulting in a total of 12 000 m² (Figure 1d). Plots in the large natural-forest fragments (ForFra) were located in VC (n = 2) and OG (n = 4) nature reserves (total fragment sizes: VC 130 ha, OG 822 ha (hereafter we always report mean ± 1 SE, if not otherwise stated), canopy cover: 89.8% ± 2.2%, altitudinal range: 220–390 m asl). Each plot within forest fragments with natural-grassland matrix (GraFra) was located in the centre of a small forest fragment in VC nature reserve that was enclosed by grassland containing isolated trees and bushes, kept open due to microclimatic conditions, grazing pressure and fire events (fragment size: 3.4 ± 1.3 ha, canopy cover: 83.8% ± 2.2%, altitudinal range: 340–480 m asl). Plots within forest fragments surrounded by eucalypt plantations (PlaFra) were situated within a 5-km stretch of native forest, which remained as a 30–50-m buffer zone of a stream within a eucalypt plantation (total stretch size: 12.6 ha, canopy cover: 70.2% ± 4.1%, altitudinal range: 480–510 m asl). Each plot within fragments with sugarcane-agriculture matrices (AgrFra) was situated within the centre of a small forest fragment embedded in large sugarcane fields (fragment size: 5.1 ± 1.3 ha, canopy cover: 85.7% ± 1.9%, altitudinal range: 390–580 m asl). Minimal distance between plots was 500 m, except for plots in PlaFra, which were at least 200 m apart. ForFra and GraFra were exposed to low human landscape modification, whereas PlaFra and AgrFra were subject to high modification.

METHODS

Arthropod community

To assess the arthropod community, we collected 10 beating samples per plot. Each beating sample consisted of 10 standardized beats on randomly selected woody seedlings and saplings in the direct surroundings of seedling/sapling subplots (Figure 1d). We used a wooden club and a fabric funnel connected to a collecting bottle filled with 70% ethyl alcohol (Sobek *et al.* 2009). Arthropods were separated from plant material and debris, preserved in 70% ethyl alcohol, identified to order and grouped into the feeding guilds predators (including parasitoids) and herbivores (Picker *et al.* 2004, Scholtz & Holm 1985). We calculated relative abundances of these two feeding guilds by dividing predator/herbivore abundances by total arthropod abundance (including decomposers) per plot.

Insect herbivory on tree recruits

In each 500-m² plot, we established 10 1-m² seedling subplots (10 m²) as well as 10 5-m² sapling subplots

(50 m²) including the seedling subplots (Figure 1d). Distance between subplots was approximately 7 m. We assessed insect herbivory on all seedlings with a diameter of < 1 cm at their base or < 75 cm height and all saplings with a diameter of < 5 cm at their base or > 75 cm height. Furthermore, we recorded the number of leaves of seedlings and saplings. Leaves of all seedlings and saplings were examined for proportions of herbivory by insects. We randomly sampled 30 leaves per plant. We defined herbivory as the removal of photosynthetic tissue (Schuldt *et al.* 2010) including loss caused by leaf chewing, galling, mining and leaf sucking. Visual estimation of proportions of herbivory was conducted by one person only (L. Fischer) to avoid estimation bias. Herbivory per seedling and sapling individual was calculated by summing up the herbivory proportions of all inspected leaves and dividing the sum by the number of inspected leaves per plant individual. To achieve a minimum sampling effort of 10 seedlings and saplings per plot, we randomly selected additional seedlings and saplings within the direct surroundings of seedling/sapling subplots, if necessary.

Forest-fragment quality

We evaluated forest-fragment quality by assessing three environmental parameters, i.e. tree diversity, vertical vegetation complexity, and relative abundance of pioneer trees. We determined tree diversity by mapping all adult trees with a diameter at breast height of > 5 cm or > 400 cm height on each 500-m² plot (Figure 1d). Species were identified using Boon (2010) and Coates Palgrave (2005); species nomenclature follows Coates Palgrave (2005; Appendix 1). Diversity of trees was calculated using the Shannon index. Moreover, tree species were classified according to their successional status as pioneer or climax species by two botanists from KZN, Tony Abbott and David Johnson, who were recommended as local experts by Dr Christina Potgieter of the Bews Herbarium of the University of KZN (pers. comm.; Appendix 1). The main criterion used for this classification was the growth rate of species (Dalling & Hubbell 2002, Laurance *et al.* 2006) combined with field experience of where species occur, e.g. species that grow quickly in a fresh open space were classified as pioneers. We determined the relative abundance of pioneer-tree species in each plot by dividing the number of pioneer individuals by total tree abundance. Furthermore, we assessed vegetation complexity on 10 25-m² subplots within the 500-m² plots including seedling/sapling subplots (Figure 1d). For this purpose, we determined the percentage cover of living biomass, consisting of woody and herbaceous vegetation, at seven horizontal layers: 0 m, 0.5 m, 1 m, 2 m, 4 m, 8 m and 16 m. We used the Shannon index to calculate

vertical vegetation complexity as suggested by Bibby *et al.* (2000) for each of the 10 subplots and averaged values for each plot.

Data analyses

All statistical analyses were performed with the program R version 2.14.1. We tested the forest-fragment-quality measures (tree diversity, vegetation complexity, pioneer trees) for collinearity using Spearman's rank correlation. Tree diversity and vegetation complexity were significantly correlated (Spearman's $\rho = 0.41$, $P = 0.045$), whereas tree diversity and pioneer trees ($\rho = 0.074$, $P = 0.73$) as well as vegetation complexity and pioneer trees ($\rho = 0.29$, $P = 0.17$) were not significantly correlated. The variable degree of human modification of the different forest-fragment types might have an effect on forest-fragment quality. Therefore, we first examined how forest-fragment quality changed with forest-fragment type applying ANOVAs. While there were significantly more pioneer trees in fragments with eucalypt plantations than in all the other forest-fragment types ($F_{3,20} = 7.19$; $P = 0.0018$), tree diversity and vegetation complexity were similarly high in all forest-fragment types. In a third step we used analyses of covariance (ANCOVA) using Type-II sums of squares to test the effects of both forest-fragment quality and forest-fragment type on abundance of arthropod predators and herbivores as well as on the proportion of herbivory on seedlings and saplings. We included the number of seedling/sapling leaves as a proxy for age as well as relative abundances of arthropod predators and herbivores into herbivory models. Fragment size was included in all models. We used the step function implemented in R for model selection to exclude independent variables and reach minimum adequate models. This selection process is based on minimizing information loss according to Akaike's Information Criterion values (Crawley 2007). We checked model residuals for normality to confirm model assumptions. We used Tukey's Honestly Significant Difference post hoc test to test for differences between forest-fragment types.

RESULTS

Arthropod community

We recorded a total of 3385 arthropods mainly consisting of insects, spiders, crustaceans and myriapods. Predators, the most abundant feeding guild ($46.9\% \pm 2.7\%$), were primarily represented by spiders, herbivores (27.1%) by Coleoptera and Hemiptera. Other arthropods, not included in these two guilds, were predominantly

decomposers, such as Collembola, crustaceans and myriapods.

The relative abundance of predators was neither affected by tree diversity nor by pioneer trees, but increased significantly with increasing vegetation complexity (Figure 2a–c, Table 1). Forest-fragment type had no significant effect on relative abundance of predators (range: 0.39 ± 0.06 in PlaFra, 0.53 ± 0.06 in GraFra; Figure 3a). The relative abundance of predators was neither affected by the relative abundance of herbivores (data not shown) nor by fragment size (Table 1).

The relative abundance of herbivores was not affected by tree diversity, but decreased significantly with increasing vegetation complexity and increased significantly with higher relative abundance of pioneer trees (Figure 2d–f, Table 1). Forest-fragment type had no effect on the relative abundance of herbivores (range: 0.22 ± 0.05 in GraFra, 0.32 ± 0.07 in AgrFra; Figure 3a). The relative abundance of herbivores was neither affected by the relative abundance of predators (data not shown) nor by fragment size (Table 1).

Insect herbivory on tree recruits

We examined a total of 9009 leaves of 897 seedling individuals belonging to 71 species and 22 686 leaves of 876 sapling individuals of 91 species. We further identified 1440 individuals of 121 tree species (see Appendix 1 for presence/absence of tree, seedling and sapling species in the different forest-fragment types).

Seedling herbivory decreased significantly with lower relative abundance of pioneer trees, but was affected neither by tree diversity nor vegetation complexity (Figure 2g–i, Table 1). Forest-fragment type had no effect on seedling herbivory, which ranged from $8.3\% \pm 1.5\%$ (PlaFra) to $11.0\% \pm 0.9\%$ (ForFra; Figure 3b, Table 1). Seedling herbivory was neither affected by the number of leaves, nor by fragment size (Table 1), nor by the relative abundance of predators or herbivores (data not shown).

Sapling herbivory was neither affected by tree diversity nor pioneer trees, whereas it increased significantly with higher vegetation complexity (Figure 2j–l, Table 1). Sapling herbivory did not vary significantly with forest-fragment type (Figure 3b, Table 1). Herbivory on saplings showed similar proportions in ForFra ($12.5\% \pm 1.4\%$), GraFra ($12.4\% \pm 0.9\%$) and AgrFra ($12.4\% \pm 1.0\%$), but was higher in PlaFra ($14.3\% \pm 2.0\%$; Figure 3b). Sapling herbivory was affected neither by the number of leaves, nor by fragment size (Table 1), nor by the relative abundances of predators or herbivores (data not shown).

DISCUSSION

To our knowledge, this is the first study to jointly address the effects of forest-fragment quality and the surrounding

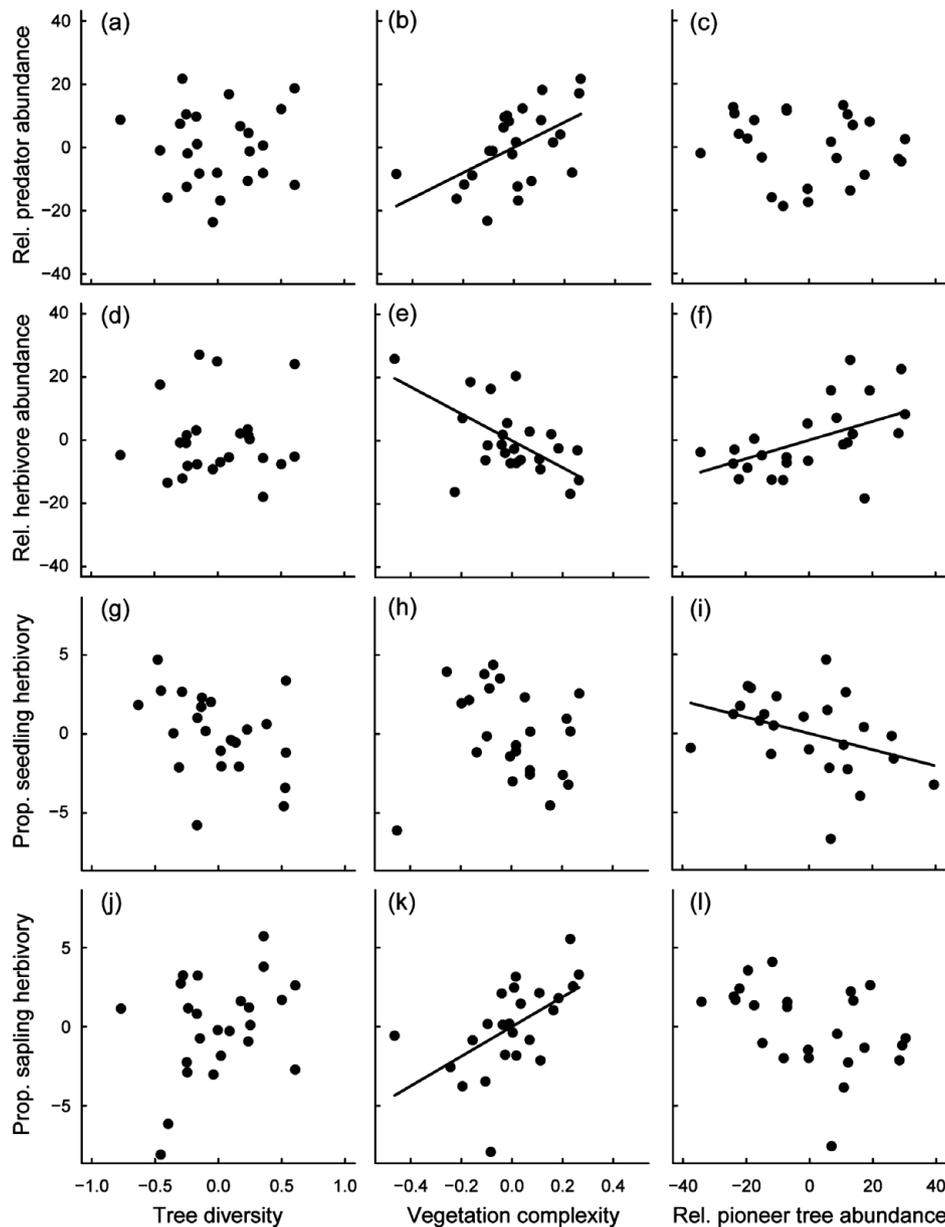


Figure 2. Arthropod and herbivory responses to forest-fragment quality in scarp-forest fragments in KwaZulu-Natal, South Africa. Partial regression plots (residuals) depicting the relationships between relative (Rel.) abundance of predators (a–c) and herbivores (d–f) and proportion (Prop.) of seedling (g–i) and sapling herbivory (j–l) in relation to tree diversity, vegetation complexity and relative abundance of pioneer trees.

matrix on arthropod communities and herbivory on woody seedlings and saplings. Our findings indicate that forest-fragment quality – especially vegetation complexity and the relative abundance of pioneer trees – strongly affects arthropods and herbivory, whereas the surrounding matrix appears to play only a minor role. Relative abundance of predators increased with higher vegetation complexity, while relative abundance of herbivores showed the opposite pattern and was also amplified by high relative abundance of pioneer trees. In contrast, seedling herbivory was reduced by high relative abundance of pioneer trees, while sapling

herbivory proliferated with intensifying vegetation complexity.

Forest-fragment quality

In line with our first hypothesis, forest fragment-quality – in terms of vegetation complexity and pioneer trees – enhanced the relative abundance of predators and reduced that of herbivores. Tree diversity per se neither affected predators nor herbivores. These findings correspond to a meta-analysis (Langellotto & Denno

Table 1. ANCOVA models testing the effects of forest-fragment quality in terms of tree diversity (Tree div.), vegetation complexity (Veg. com.), relative abundance of pioneer trees (Pioneers), and forest-fragment type (Frag. type) as well as fragment size (Frag. size) and number of seedling/sapling leaves (No. leaves) on relative abundances of arthropods (predators, herbivores) and insect herbivory on woody seedlings and saplings in scarp-forest fragments in KwaZulu-Natal, South Africa. Given are df-, R²-, F- and P-values for full models after stepwise deletion of non-significant terms (ns); – = excluded from model, na = not applicable; * = P < 0.05, ** = P < 0.01.

	Relative abundance of arthropods						Herbivory					
	Predators			Herbivores			Seedlings			Saplings		
	R ²	df	F	R ²	df	F	R ²	df	F	R ²	df	F
Full model	0.25	2,21	4.91*	0.42	4,19	5.15**	0.38	3,20	5.68**	0.27	6,17	2.45 ^{ns}
Tree div.	–	–	–	–	1	2.08 ^{ns}	–	1	3.45 ^{ns}	–	–	–
Veg. com.	–	–	–	–	1	10.9**	–	–	–	–	1	7.27*
Pioneers	–	–	–	–	1	13.0**	–	–	–	–	1	3.78 ^{ns}
Frag. type	–	–	–	–	–	–	–	–	–	–	3	3.09 ^{ns}
Frag. size	–	–	–	–	1	2.15 ^{ns}	–	–	–	–	1	4.32 ^{ns}
No. leaves	–	–	–	–	na	na	–	1	2.08 ^{ns}	–	–	–

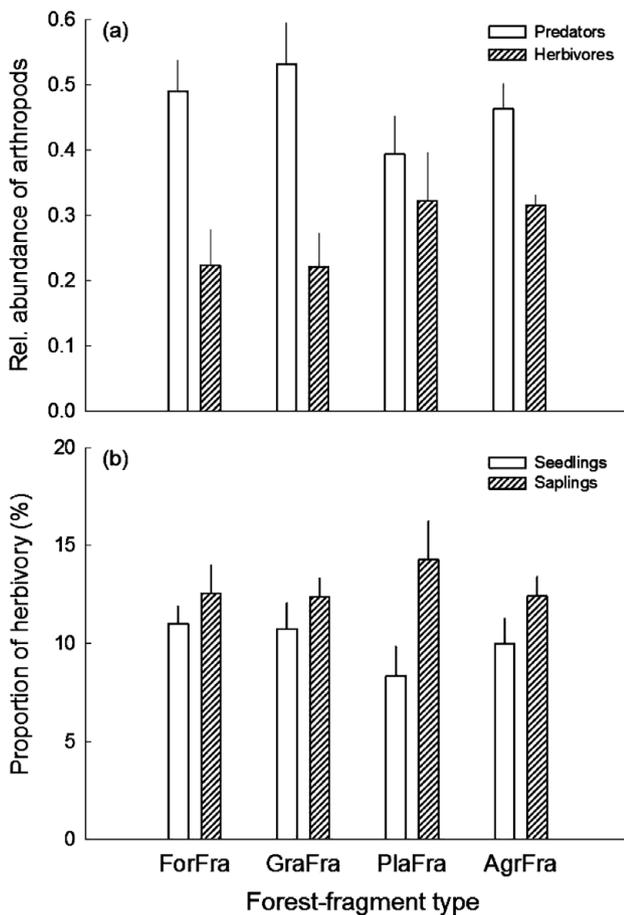


Figure 3. Arthropod and herbivory responses to different scarp-forest-fragment types in large natural-forest fragments (ForFra), small natural-forest fragments surrounded by grassland (GraFra) and in small modified-forest fragments surrounded by eucalypt plantations (PlaFra) and sugarcane agriculture (AgrFra) in KwaZulu-Natal, South Africa. Relative abundances of arthropod predators (white) and herbivores (filled; a) and proportions of herbivory on woody seedlings (white) and saplings (filled; b) as percentage leaf area loss. Shown are means (+ SE).

2004) and support the structural complexity argument of the ‘enemies hypothesis’ – higher diversity involves an increase in structural and resource diversity for natural enemies like arthropod predators (Root 1973). In our study the combination of high structural complexity and high tree diversity seemed to provide diverse shelter and resource opportunities to support a predator community that regulated insect herbivores via top-down regulation.

As we expected, relative abundance of herbivores increased with higher relative abundance of pioneer trees. This phenomenon has been ascribed to enhanced resource quality, i.e. higher foliage palatability and nutritive value of pioneer plants, which are consequently more attractive to herbivores (Richards & Coley 2007, Ruiz-Guerra *et al.* 2010, Wirth *et al.* 2008). Thus, in our community-wide approach, structural components of the habitat as well as tree community composition in terms of successional status appear to be more important for arthropod abundances than tree diversity per se.

Responses of herbivory on tree recruits varied: vegetation complexity amplified sapling herbivory and relative abundance of pioneer trees decreased seedling herbivory. Sapling herbivory increased with higher vegetation complexity, which correlated with tree diversity. Such a positive diversity–herbivory relationship diverges from the concept of ‘associational resistance’ expecting reduced herbivory in diverse and complex systems (Root 1973). However, the opposite, which we found – diversity and complexity increase herbivory – has been attributed to a spillover of generalist herbivores from preferred host plants to adjacent non-host plants (‘associational susceptibility’, White & Whitham 2000). Similar to our results, Schuldt *et al.* (2010) found a positive diversity–herbivory relationship for saplings in comparably diverse subtropical forests in China and explained this with a strong impact of generalist herbivores in their system. Generalist herbivores have been shown to benefit from the higher resource availability in diverse systems (Jactel & Brockerhoff 2007).

The decrease of seedling herbivory with a higher relative abundance of pioneer trees contrasts with our expectation and recent findings of others (Ruiz-Guerra *et al.* 2010, Wirth *et al.* 2008). Potentially, other detrimental edge effects mitigated the intensification of herbivory owing to a higher relative abundance of more palatable pioneer trees. For instance, Valladares *et al.* (2006) reported lower herbivory rates at forest edges compared with the interior and attributed this to microclimatic changes, such as higher variability in temperature, increased light intensity and lower humidity, near edges. However, as this speculation contradicts the increase of herbivore abundance with pioneer trees, a more plausible explanation might be that our herbivore community predominantly consisted of generalists rather than specialists – as also argued in the case of sapling herbivory. High relative abundance of pioneer trees correlated positively with herbaceous ground vegetation cover (Botzat *et al.*, unpubl. data). We therefore assume a spillover of generalist herbivores from woody seedlings and saplings to the herbaceous vegetation. In summary, herbivory on woody seedlings and saplings seemed to be driven by associational susceptibility (spillover) rather than by associational resistance (natural enemies).

One possible reason for contrasting responses of arthropods and herbivory to forest-fragment quality might be the rather weak trophic relationships in forest fragments between arthropod predators and herbivores. The scarp-forest fragments have existed since the last glacial maximum (Eeley *et al.* 1999, Lawes *et al.* 2005). In such natural systems, species with stronger defence against predators/herbivores might have become more dominant over time and species interactions might be weak and diffuse (Leibold *et al.* 1997, Polis *et al.* 2000). Top-down regulation is believed to be much stronger in simple systems (Polis *et al.* 2000), whereas in complex systems it might be constrained due to higher stability and redundancy (McCann *et al.* 1998, Polis *et al.* 2000). Another possible explanation for no herbivore–herbivory effect might be altered herbivore species compositions and functional diversity, which we did not consider with our abundance data. For instance, modified proportions of generalist and specialist herbivores leading to the increase of key herbivores might considerably impact herbivory (Haynes & Crist 2009).

Matrix habitat

Not supporting our second prediction, arthropod abundances did not differ among forest-fragment types. This result is in contrast with, for example, Steffan-Dewenter (2003) who found an increase of predator species with landscape diversity in the matrix. These negligible matrix effects on arthropods and herbivory

correspond to findings of a recent meta-analysis, in which Chaplin-Kramer *et al.* (2011) came to the conclusion that although predators clearly respond positively to landscape complexity, this does not implicitly mean a reduction in herbivory. Likewise, Haynes & Crist (2009) reported neither an effect of matrix composition, nor of fragmentation on insect herbivory.

Based on these considerably weak matrix effects, we presume that neither predator, nor herbivore dispersal were strongly hampered by matrix habitat. This emphasizes our assumption that the arthropod community in our study system rather consisted of generalist species that may be able to cope with matrices in general or even benefit from the higher dietary mixture (Haynes & Crist 2009, Schuldt *et al.* 2010). Therefore, even modified matrices might to some extent facilitate dispersal of generalist arthropods among scarp-forest fragments. However, human-modified matrices in many cases lack structural complexity, which has been shown to be important for arthropod predators and their role in insect herbivore control (Tscharntke *et al.* 2007). Thus, in order to determine matrix permeability for arthropods, further research should apply qualitative measures, such as the index of functional landscape heterogeneity proposed by Fahrig *et al.* (2011), which seems to be a promising tool to integrate variable species requirements at a landscape scale.

Conclusions

In conclusion, relative abundances of arthropod predators and herbivores as well as insect herbivory on woody seedlings and saplings appeared to be most distinctly shaped by forest-fragment quality. Thus, in order to sustain complex ecological processes involving predators, herbivores and herbivory in fragmented landscapes, the quality of forest fragments should be considered. High vegetation complexity seems to support arthropod predator communities that regulate herbivores. However, partly diverging herbivory responses suggest trophic interactions between arthropods and herbivory to be weak and diffuse in scarp-forest fragments. Future studies that consider species identities and functional roles of arthropods might help to explain missing direct relationships between arthropods and herbivory. Though matrix effects were of lower importance, human-modified matrices lacking structural complexity might have the potential to hamper insect control by arthropod predators and thereby negatively affect plant performance. Here, in-depth studies within matrices that consider measures of functional landscape heterogeneity might clarify the role of the matrix for the complex interactions between arthropods and woody seedling and sapling herbivory in forest fragments.

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Appendix 1. Successional status (Succ.: P = pioneer, C = climax) and presence (+) or absence (–) of tree (tr), seedling (se) and sapling (sa) species in large natural-forest fragments (ForFra), small natural-forest fragments surrounded by grassland (GraFra) and in small modified-forest fragments surrounded by plantations (PlaFra) and agriculture (AgrFra) in KwaZulu-Natal, South Africa.

Forest-fragment type	Species (family)	Succ.	ForFra			GraFra			PlaFra			AgrFra		
			tr	se	sa									
<i>Acacia caffra</i> (Fabaceae)	C	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Acacia mearnsii</i> (Fabaceae)	P	–	–	–	–	+	+	–	+	+	–	–	–	
<i>Acalypha glabrata</i> var. <i>glabrata</i> (Euphorbiaceae)	P	+	+	+	–	–	–	–	–	–	+	–	–	
<i>Acokanthera oppositifolia</i> (Apocynaceae)	C	–	–	+	–	–	–	–	–	–	+	–	+	
<i>Acridocarpus natalitius</i> var. <i>natalitius</i> (Malpighiaceae)	C	–	–	+	–	–	–	–	–	–	–	–	–	
<i>Albizia adianthifolia</i> var. <i>adianthifolia</i> (Fabaceae)	P	+	–	–	–	–	–	–	–	–	+	–	+	
<i>Allophylus africanus</i> var. <i>africanus</i> (Sapindaceae)	P	+	–	–	–	+	–	–	+	–	+	–	+	
<i>Allophylus dregeanus</i> (Sapindaceae)	P	–	–	–	+	+	–	+	+	–	+	–	–	
<i>Antidesma venosum</i> (Euphorbiaceae)	P	+	–	–	–	–	–	–	–	–	+	–	–	
<i>Apodytes dimidiata</i> subsp. <i>dimidiata</i> (Icacinales)	P	–	–	–	+	–	–	+	–	–	+	+	+	
<i>Bachmannia woodii</i> (Capparaceae)	C	–	–	+	–	–	–	–	–	–	–	–	–	
<i>Baphia racemosa</i> (Fabaceae)	C	+	+	+	–	–	–	–	–	–	–	–	–	
<i>Bersama swinnyi</i> (Melianthaceae)	C	–	–	–	–	–	–	–	–	–	+	–	–	
<i>Bersama tysoniana</i> (Melianthaceae)	C	+	–	–	–	–	–	–	–	–	+	+	–	
<i>Brachylaena discolor</i> (Asteraceae)	C	–	–	–	–	–	–	–	–	–	+	–	–	
<i>Brachylaena elliptica</i> (Asteraceae)	C	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Brachylaena uniflora</i> (Asteraceae)	C	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Bridelia micrantha</i> (Euphorbiaceae)	C	+	–	–	–	–	–	–	–	–	+	–	–	
<i>Burchellia bubalina</i> (Rubiaceae)	C	–	–	–	–	–	–	–	–	–	–	–	+	
<i>Calodendrum capense</i> (Rutaceae)	C	–	–	–	–	–	–	–	–	–	+	–	–	
<i>Calpurnia aurea</i> subsp. <i>aurea</i> (Fabaceae)	P	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Canthium ciliatum</i> (Rubiaceae)	C	–	–	–	–	+	+	–	+	+	+	+	+	
<i>Canthium inerme</i> (Rubiaceae)	C	+	–	–	–	–	–	–	–	–	+	–	+	
<i>Canthium spinosum</i> (Rubiaceae)	P	+	–	–	+	–	+	+	–	+	+	–	+	
<i>Canthium suberosum</i> (Rubiaceae)	C	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Carissa macrocarpa</i> (Apocynaceae)	P	–	–	–	–	–	–	–	–	–	+	–	–	
<i>Cassine peragua</i> subsp. <i>peragua</i> (Celastraceae)	P	–	–	–	–	–	–	–	–	–	–	+	–	
<i>Cassipourea gunniflora</i> var. <i>verticillata</i> (Rhizophoraceae)	C	+	+	–	–	–	–	–	–	–	–	–	–	
<i>Cassipourea malosana</i> (Rhizophoraceae)	C	+	–	+	–	–	–	–	–	–	+	–	–	
<i>Caturanegam obovata</i> (Rubiaceae)	P	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Celtis africana</i> (Celtidaceae)	P	+	+	–	+	+	+	+	+	+	+	–	–	
<i>Cestrum laevigatum</i> (Solanaceae)	P	–	–	–	+	+	+	+	+	+	–	–	–	
<i>Chaetachme aristata</i> (Celtidaceae)	C	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Clausena anisata</i> (Rutaceae)	P	+	+	–	–	–	–	–	–	–	+	–	+	
<i>Clerodendrum glabrum</i> var. <i>glabrum</i> (Lamiaceae)	P	+	–	–	+	–	+	+	–	+	+	–	–	
<i>Cnestis polyphylla</i> (Connaraceae)	C	–	–	–	–	+	+	–	+	+	–	–	+	
<i>Combretum erythrophyllum</i> (Combretaceae)	P	+	–	–	+	+	+	+	+	+	+	+	+	
<i>Combretum kraussii</i> (Combretaceae)	C	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Commiphora harveyi</i> (Bursaceae)	C	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Commiphora woodii</i> (Bursaceae)	C	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Croton sylvaticus</i> (Euphorbiaceae)	P	+	–	–	+	–	–	+	–	–	+	–	–	
<i>Cryptocaria myrtifolia</i> (Lauraceae)	C	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Cryptocaria woodii</i> (Lauraceae)	C	–	–	–	–	–	–	–	–	–	+	–	+	
<i>Cryptocaria wyliei</i> (Lauraceae)	P	–	–	–	–	–	–	–	–	–	+	–	+	
<i>Cunonia capensis</i> (Cunoniaceae)	P	–	–	–	–	–	–	–	–	–	–	+	–	
<i>Cussonia sphaerocephala</i> (Araliaceae)	C	+	–	–	–	–	–	–	–	–	+	–	–	
<i>Cussonia spicata</i> (Araliaceae)	P	+	–	–	–	–	–	–	–	–	+	–	–	
<i>Deinbollia oblongifolia</i> (Sapindaceae)	P	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Diospyros lycioides</i> subsp. <i>sericea</i> (Ebenaceae)	P	+	+	+	+	–	+	+	–	+	+	–	–	
<i>Diospyros villosa</i> var. <i>villosa</i> (Ebenaceae)	P	–	–	–	+	–	–	+	–	–	–	–	–	
<i>Dombeya burgessiae</i> (Sterculiaceae)	P	+	–	–	–	–	–	–	–	–	–	+	–	
<i>Dombeya tiliaceae</i> (Sterculiaceae)	P	–	–	–	–	–	+	–	–	+	–	–	–	
<i>Dovyalis lucida</i> (Flacourtiaceae)	P	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Dovyalis rhamnoides</i> (Flacourtiaceae)	P	–	–	–	+	+	+	+	+	+	+	–	–	
<i>Dracaena alectrifomis</i> (Dracaenaceae)	P	+	–	–	+	+	+	+	+	+	+	–	+	
<i>Drypetes arguta</i> (Euphorbiaceae)	C	+	+	+	–	–	–	–	–	–	–	–	+	
<i>Drypetes gerrardii</i> var. <i>gerrardii</i> (Euphorbiaceae)	C	+	+	–	+	–	–	+	–	–	+	+	+	
<i>Ekebergia capensis</i> (Meliaceae)	P	–	–	–	–	–	–	–	–	–	+	–	–	

Appendix 1. Continued

Forest-fragment type Species (family)	Succ.	ForFra			GraFra			PlaFra			AgrFra		
		tr	se	sa									
<i>Elaeodendron croceum</i> (Celastraceae)	P	+	+	+	-	-	-	-	-	-	+	-	+
<i>Englerophytum natalense</i> (Sapotaceae)	C	+	+	+	-	-	-	-	-	-	+	-	-
<i>Erythrina caffra</i> (Fabaceae)	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Erythrina lysistemon</i> (Fabaceae)	P	-	-	-	-	-	+	-	-	+	-	-	-
<i>Erythrococca</i> sp. nov. (Euphorbiaceae)	C	-	-	-	-	-	-	-	-	-	+	-	-
<i>Eucalyptus grandis</i> (Myrtaceae)	P	-	-	-	+	-	-	+	-	-	-	-	-
<i>Euclea natalensis</i> subsp. <i>natalensis</i> (Ebenaceae)	C	-	-	-	-	-	-	-	-	-	+	-	+
<i>Eugenia natalitia</i> (Myrtaceae)	C	-	-	-	+	-	+	+	-	+	+	-	+
<i>Eugenia umtamvunensis</i> (Myrtaceae)	C	+	+	+	-	+	-	-	+	-	-	-	-
<i>Eugenia woodii</i> (Myrtaceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Faurea saligna</i> (Proteaceae)	P	-	-	-	-	-	+	-	-	+	-	-	-
<i>Ficus burkei</i> (Moraceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Ficus burtt-davyi</i> (Moraceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Ficus craterostoma</i> (Moraceae)	C	-	-	-	+	-	-	+	-	-	+	-	-
<i>Ficus natalensis</i> subsp. <i>natalensis</i> (Moraceae)	P	+	-	-	-	-	-	-	-	-	+	-	-
<i>Ficus sur</i> (Moraceae)	P	-	-	-	+	-	-	+	-	-	+	-	-
<i>Gardenia thunbergia</i> (Rubiaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Grewia lasiocarpa</i> (Tiliaceae)	C	-	-	-	+	+	+	+	+	+	+	-	+
<i>Grewia occidentalis</i> var. <i>occidentalis</i> (Tiliaceae)	P	-	-	-	+	-	-	+	-	-	+	-	-
<i>Gymnosporia buxifolia</i> (Celastraceae)	P	-	-	-	-	-	-	-	-	-	+	-	-
<i>Gymnosporia harveyana</i> (Celastraceae)	C	+	-	-	-	-	-	-	-	-	+	+	+
<i>Gymnosporia nemorosa</i> (Celastraceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Halleria lucida</i> (Scrophulariaceae)	P	-	-	-	+	-	+	+	-	+	+	-	+
<i>Harpephyllum caffrum</i> (Anacardiaceae)	C	-	-	-	-	-	-	-	-	-	+	-	-
<i>Heywoodia lucens</i> (Euphorbiaceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hippobromus pauciflorus</i> (Sapindaceae)	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyperacanthus amoenus</i> (Rubiaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Kiggelaria africana</i> (Flacourtiaceae)	P	-	-	-	+	-	+	+	-	+	-	-	-
<i>Macaranga capensis</i> (Euphorbiaceae)	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Maerua cafra</i> (Capparaceae)	P	-	-	-	-	-	-	-	-	-	+	-	+
<i>Maesa lanceolata</i> (Maesaceae)	P	+	-	-	+	+	+	+	+	+	+	-	+
<i>Margaritaria discoidea</i> var. <i>fagifolia</i> (Euphorbiaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Maytenus abottii</i> (Celastraceae)	P	-	-	-	-	-	-	-	-	-	+	-	+
<i>Maytenus acuminata</i> (Celastraceae)	P	-	-	-	-	+	-	-	+	-	-	-	-
<i>Maytenus peduncularis</i> (Celastraceae)	C	-	-	-	-	-	-	-	-	-	+	-	-
<i>Maytenus undata</i> (Celastraceae)	P	-	-	-	+	-	-	+	-	-	-	-	-
<i>Memecylon natalense</i> (Melastomataceae)	C	-	+	-	-	-	-	-	-	-	-	-	-
<i>Millettia grandis</i> (Fabaceae)	P	+	+	+	-	-	-	-	-	-	-	-	-
<i>Mimusops obovata</i> (Sapotaceae)	C	+	-	-	-	-	-	-	-	-	+	-	-
<i>Nectaropetalum capense</i> (Erythroxylaceae)	C	+	-	+	-	-	-	-	-	-	-	-	-
<i>Obetia tenax</i> (Urticaceae)	P	+	-	+	-	-	-	-	-	-	+	-	-
<i>Ochna arborea</i> var. <i>arborea</i> (Ochnaceae)	C	+	+	+	-	-	-	-	-	-	-	-	-
<i>Ochna serrulata</i> (Ochnaceae)	P	-	-	+	-	+	-	-	+	-	-	+	-
<i>Olea capensis</i> subsp. <i>macrocarpa</i> (Oleaceae)	C	-	-	+	-	-	-	-	-	-	-	-	-
<i>Oricia bachmannii</i> (Rutaceae)	C	+	-	+	-	-	-	-	-	-	-	-	-
<i>Pavetta bowkeri</i> (Rubiaceae)	C	-	-	-	-	+	-	-	+	-	-	-	+
<i>Pavetta lanceolata</i> (Rubiaceae)	P	-	-	-	+	+	+	+	+	+	+	-	-
<i>Peddiea africana</i> (Thymelaeaceae)	C	+	+	-	+	+	+	+	+	+	-	+	+
<i>Phoenix reclinata</i> (Arecaceae)	P	+	+	+	-	+	+	-	+	+	-	-	-
<i>Pittosporum viridiflorum</i> (Pittosporaceae)	P	+	-	-	-	-	-	-	-	-	+	-	+
<i>Pleurostyliia capensis</i> (Celastraceae)	C	+	-	+	+	-	-	+	-	-	+	-	+
<i>Podocarpus latifolius</i> (Anacardiaceae)	C	-	-	-	-	+	+	-	+	+	-	-	-
<i>Protorhus longifolia</i> (Celastraceae)	P	+	+	-	+	+	+	+	+	+	+	+	+
<i>Pseudoscolopia polyantha</i> (Flacourtiaceae)	P	-	-	-	-	-	+	-	-	+	-	-	-
<i>Psychotria capensis</i> subsp. <i>capensis</i> (Rubiaceae)	P	+	-	+	+	+	+	+	+	+	+	+	+
<i>Rapanea melanophloeos</i> (Myrsinaceae)	P	+	-	+	-	-	-	-	-	-	+	+	+
<i>Rauvolfia caffra</i> (Apocynaceae)	P	+	+	-	-	-	-	-	-	-	-	-	-
<i>Rawsonia lucida</i> (Flacourtiaceae)	C	-	-	-	-	-	-	-	-	-	-	-	-
<i>Searsia chiridensis</i> (Anacardiaceae)	P	+	-	-	+	-	-	+	-	-	+	-	+
<i>Searsia dentata</i> (Anacardiaceae)	P	-	-	-	-	-	-	-	-	-	+	-	+
<i>Rothmannia globosa</i> (Rubiaceae)	C	+	-	-	-	-	-	-	-	-	+	+	+

Appendix 1. Continued

Forest-fragment type Species (family)	Succ.	ForFra			GraFra			PlaFra			AgrFra		
		tr	se	sa									
<i>Schrebera alata</i> (Oleaceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Scolopia zeyheri</i> (Flacourtiaceae)	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Strelitzia nicolai</i> (Strelitziaceae)	P	+	-	+	+	-	+	+	-	+	-	-	-
<i>Strychnos decussata</i> (Strychnaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Strychnos hemingsii</i> (Strychnaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Strychnos usambarensis</i> (Strychnaceae)	C	+	+	+	-	-	-	-	-	-	-	-	-
<i>Syzygium cordatum</i> (Myrtaceae)	P	+	-	-	+	-	+	+	-	+	+	-	-
<i>Vangueria parviflora</i> (Rubiaceae)	P	-	-	-	-	-	+	-	-	+	-	-	-
<i>Tarena pavettooides</i> subsp. <i>pavettooides</i> (Rubiaceae)	P	+	+	-	-	-	-	-	-	-	-	-	-
<i>Teclea gerrardii</i> (Rutaceae)	C	+	-	-	-	-	-	-	-	-	-	-	-
<i>Teclea natalensis</i> (Rutaceae)	C	+	+	-	-	-	-	-	-	-	-	-	-
<i>Trema orientalis</i> (Celtidaceae)	P	-	-	-	+	+	-	+	+	-	+	-	-
<i>Tricalysia capensis</i> var. <i>capensis</i> (Rubiaceae)	P	-	-	-	-	-	-	-	-	-	+	-	+
<i>Tricalysia sonderiana</i> (Rubiaceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Trichilia dregeana</i> (Meliaceae)	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vangueria infausta</i> (Rubiaceae)	P	-	-	-	-	-	+	-	-	+	+	-	-
<i>Vepris lanceolata</i> (Rutaceae)	P	-	-	-	+	-	-	+	-	-	+	+	+
<i>Xylothea kraussiana</i> (Flacourtiaceae)	P	+	-	-	-	-	-	-	-	-	-	-	-
<i>Xymalos monospora</i> (Monimiaceae)	C	-	-	-	-	-	-	-	-	-	-	-	-
<i>Zanthoxylum capense</i> (Rutaceae)	P	-	-	-	+	-	+	+	-	+	+	-	-
<i>Zanthoxylum davyi</i> (Rutaceae)	C	-	-	-	-	-	-	-	-	-	-	-	+