

Fragment quality rather than matrix habitat
shapes forest regeneration
in a South African mosaic-forest landscape

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Saskia C. Morgenstern

'Humanity has always been, and always will be, a part of nature.'

(Gretchen C. Daily)

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1 General introduction

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Mosaic-forest landscapes

Land-use change and agricultural intensification are responsible for a global decline of forest cover entailing the continuous fragmentation of forests (Saunders *et al.* 1991; Fahrig 2003; Green *et al.* 2005). Forest fragments are characterized by reduced habitat size and exhibit strong edge effects, which cause changes in abiotic factors, such as higher light intensity on the forest floor or altered air temperature and thereby potentially affect their habitat quality (Murcia 1995; Laurance *et al.* 2002). Several studies have illustrated that forest fragmentation is one of the main drivers of biodiversity loss and consequently alters key ecological processes, *e.g.* seed predation, seedling establishment and herbivory (Donoso *et al.* 2003; Benítez-Malvido & Martínez-Ramos 2003a; Benítez-Malvido & Lemus-Albor 2005). Nevertheless, forest fragments can contribute to landscape connectivity, provide habitat for numerous animal species and are thus important stepping-stones for maintaining ecological processes (Estrada & Coates-Estrada 2002; Bodin *et al.* 2006; Fischer & Lindenmayer 2007). Especially in areas that now lack continuous natural forests, fragments enhance the diversity of the landscape and increase chances of species survival (Turner & Corlett 1996).

Traditionally matrices surrounding fragments have been perceived as inhospitable oceans of no value to species conservation. This included a binary view of landscapes distinguishing between habitat and non-habitat (*e.g.* Murphy & Lovett-Doust 2004 and references therein). In fact, matrices surrounding forest fragments vary in structure and permeability for different species (Kupfer *et al.* 2006; Brockerhoff *et al.* 2008 and references therein). High-contrast matrices differing strongly in structure from the original habitat might hinder species movement and plant-animal interactions (Prevedello & Vieira 2010; Herrera *et al.* 2011). Contrarily, low-contrast matrices that are structurally similar to the natural habitat might facilitate species and propagule dispersal and thereby contribute to the stability of human-modified fragmented landscapes (Tewksbury *et al.* 2002; Herrera & García 2009).

Overall, forest fragmentation involves the creation of a ‘mosaic’ landscape with remnants of natural habitat within variable matrix habitat (Fahrig 2003). Inspired by two well-established ecological theories—*island biogeography* and *metapopulation theory*—it was believed that the conservation of many species could only be accomplished in large habitat patches as species richness is likely to increase with habitat area and connectivity

(MacArthur & Wilson 1967; Hanski & Ovaskainen 2000). Nowadays, an integrated perspective of landscapes is favoured by many conservation scientists highlighting the great potential of human-modified mosaic-forest landscapes comprising both small forest fragments as well as matrix habitat for biodiversity conservation and for maintaining ecological processes (Daily 2001; Jules & Shahani 2003).

FOREST REGENERATION IN MOSAIC LANDSCAPES. Forest regeneration is a complex process of subsequent transitions from one stage of establishment to the next (Wang & Smith 2002). Thus, it forms the template for all processes that enforce plant recruitment. For instance, animal-mediated seed dispersal enables the transportation of seeds away from the mother plant, where density-dependent mortality of seeds and seedlings is high (Janzen 1970; Connell 1971). Once dispersed, seeds are exposed to seed predators, *e.g.* rodents or insects or are secondarily dispersed by scatter-hoarding animals (*e.g.* Forget 1996). The subsequent establishment of seedlings is not only affected by biotic factors, *i.e.* seed dispersal, predation and vegetational characteristics, it is also determined by abiotic factors, such as light availability (Sork 1987). Lastly, survival to the sapling stage and long-term establishment are strongly influenced by herbivore and pathogen pressure (Wang & Smith 2002).

Ongoing forest fragmentation involving the formation of matrix habitat has been shown to alter communities of seed dispersers, seed predators, herbivores and plants (*e.g.* Cordeiro & Howe 2001; Donoso *et al.* 2003; Benítez-Malvido & Lemus-Albor 2005). Further, abiotic conditions may lead to unfavourable conditions in fragmented forests and their matrix habitat may vary in permeability for different species (Laurance *et al.* 2002; Prevedello & Vieira 2010). This in turn may crucially affect the complex processes of forest regeneration. Therefore, it is pivotal to identify the consequences of human-induced forest fragmentation for biodiversity and ecological processes involved in forest regeneration.

Rodent seed predation in mosaic-forest landscapes

Seed predation is a fundamental antagonistic plant-animal interaction, once seeds have reached the ground. It has consequences for seed survival, seedling establishment and eventually forest regeneration (Stoner *et al.* 2007; Farwig *et al.* 2008a). Especially in (sub-) tropical forests seeds suffer high predation rates and seed predation has been described as a

bottleneck between seed production and seedling recruitment (Wenny 2000). Seed predators can be insects, birds and mammals (Janzen 1971). Particularly rodents are important drivers of seed predation with predation rates exceeding those of insects (Cole 2009). Accordingly, high rodent abundance has proven to entail elevated seed predation pressure in forest ecosystems (Tallmon *et al.* 2003).

Human activities, leading to forest fragmentation and the formation of matrix habitat, have been shown to affect seed predator communities and seed predation (Donoso *et al.* 2003; Umetsu & Pardini 2007). For instance, edge effects in forest fragments cause a high light intensity on the forest floor entailing an increase of herbal ground vegetation cover, which might enhance forest fragmentation quality for rodent communities (Hay & Fuller 1981; Mortelliti & Boitani 2006). Resulting increased rodent abundances have been shown to cause elevated seed predation in small forest fragments (Santos & Tellería 1994; García & Chacoff 2007), thereby ultimately influencing seedling establishment (Asquith *et al.* 1997).

Moreover, the surrounding matrix habitat might directly or indirectly influence rodent communities. Dispersal of rodents as well as that of their predators might be facilitated or impeded depending on the species-specific permeability of the matrix (Ricketts 2001; Kupfer *et al.* 2006). For example, many studies have shown that rodents might become ecologically released due to a decline of their top predators in fragmented landscapes (*e.g.* Terborgh *et al.* 2008). Furthermore, the matrix might hamper seed disperser movement among forest fragments, which might cause the accumulation of seeds underneath the parent plant and in this way indirectly favour seed predators (Janzen 1970; Connell 1971). Consequently, forest fragmentation and matrix habitat may create beneficial conditions for rodents, which are important determinants of seed predation, and may thereby have the potential to modify seedling establishment and forest regeneration.

Establishment of woody seedlings and saplings in mosaic-forest landscapes

Forest regeneration hinges on the availability of seeds and their ability to survive and establish (Benítez-Malvido & Martínez-Ramos 2003a). The presence of seeds is strongly determined by seed dispersal and predation. As forest fragmentation may alter seed

disperser and predator communities, this might in turn limit the availability of seeds and accordingly also negatively affect seedling diversity and abundance (Sizer & Tanner 1999; Benítez-Malvido & Martínez-Ramos 2003a). Consequently, maintaining tree diversity might be impeded in fragmented tree communities (Wright & Duber 2001).

Several studies have investigated the influence of forest fragmentation on forest regeneration processes, such as seedling and sapling establishment (Benítez-Malvido 1998; Benítez-Malvido & Martínez-Ramos 2003a). Most of them revealed diminished seedling species richness and abundance, often due to changes in abiotic factors, *e.g.* edge effects with negative consequences for forest fragment quality (Saunders *et al.* 1991; Sizer & Tanner 1999; Benítez-Malvido & Martínez-Ramos 2003b). Moreover, biotic interactions may be altered in fragmented forests. For example, the decline of top predators in forest fragments might lead to the release of seed predators or herbivores with negative consequences for seedling establishment (Terborgh *et al.* 2008). Yet, not only species richness and abundance, but also species composition of tree recruits might be affected by forest fragmentation (Tabarelli *et al.* 2004; Laurance *et al.* 2006). Numerous studies have detected a compositional shift in successional status with an increase of early-successional species in fragments at the expense of late-successional species, presumably caused by higher light intensity near forest edges (Benítez-Malvido & Martínez-Ramos 2003b; Farwig *et al.* 2008b; Kirika *et al.* 2010).

In addition to abiotic and biotic modifications within forest fragments the role of the matrix habitat for forest regeneration has been acknowledged (Nascimento *et al.* 2006). Depending on its permeability, it might permit or obstruct the movement of, *e.g.* seed dispersers and thus mediate seed influx (Estrada & Coates-Estrada 2001; Melo *et al.* 2010). In this regard, structurally complex landscapes might contribute to the functional connectivity of forest fragments (Tewksbury *et al.* 2002). Therefore, the study of tree diversity and seedling and sapling establishment, considering the role of different matrices enclosing forest fragments, provides crucial information on human impact on forest regeneration.

Leaf damage of woody seedlings and saplings in mosaic-forest landscapes

Successful establishment of woody seedlings and saplings can be strongly hampered by insect herbivory and leaf pathogen infestation. As herbivores and pathogens can impact survival, growth and productivity of plant individuals, they also have the potential to affect the structure and regeneration dynamics of forests (Burdon 1993; Maron & Crone 2006).

Forest fragmentation may modify patterns of herbivory and pathogen infestation (Krüss & Tschardt 1994; Santos & Benítez-Malvido 2012). For instance, the structural quality of forest fragments may be influential for arthropods, especially predators, and might thus also affect insect herbivory (Langellotto & Denno 2004; Janssen *et al.* 2007). This can partly be attributed to a decline of tree diversity in disturbed forests (*e.g.* Jactel & Brockerhoff 2007; Haas *et al.* 2011). Diverse communities have been shown to be less susceptible to insect herbivory, which is referred to as ‘associational resistance’. This has been elucidated with two well-established concepts: the ‘resource concentration hypothesis’ and the ‘enemies hypothesis’. The first one predicts a decrease in herbivory with increasing tree diversity because specialist herbivores fail to detect their hosts as diversity increases (Tahvanai & Root 1972; Root 1973). The second hypothesis presumes that higher diversity entails the increase of structural and resource diversity. Such additional shelter and food for natural enemies might lead to top-down control of herbivores, which in turn potentially lessens herbivory (Root 1973; Terborgh *et al.* 2001). Contrary effects of enhanced vulnerability of diverse plant communities to insect herbivory have been reported as a result of higher dietary choice or spillover of generalist herbivores to non-host plants, named ‘associational susceptibility’ (White & Whitham 2000; Unsicker *et al.* 2008). Diversity effects on pathogen infestation are similarly variable. In most studies pathogen transmission declined in diverse systems due to higher competition and reduced densities of host species (*e.g.* Mitchell *et al.* 2002; Roscher *et al.* 2007). However, diversity might also amplify pathogen infestation as high plant diversity might involve a wide host range for pathogens (Keesing *et al.* 2010). Fragmentation effects on pathogen infestation have rarely been studied (but see Benítez-Malvido *et al.* 1999; Holdenrieder *et al.* 2004). One reason for this is that pathogens largely depend on their hosts, which might be more susceptible to diseases in fragmented landscapes. Further, pathogen transmission might also be obstructed by fragmentation (Jules *et al.* 2002; Holdenrieder *et al.* 2004).

In addition to the quality of forest fragments the matrix habitat may be relevant to insect herbivory and leaf pathogen infestation. The matrix may permit or impede the movement of insectivorous vertebrate predators and thereby enhance or reduce herbivore control (*e.g.* Kalka *et al.* 2008). Moreover, the matrix may offer complementary resources for both arthropod predators and herbivores (Haynes *et al.* 2007). In consequence, assessing the impact of forest fragment quality and matrix habitat on arthropod predator and herbivore abundance, insect herbivory and leaf fungal pathogen infestation might contribute to a better understanding of plant-herbivore and plant-pathogen interactions in fragmented forests.

Aims and outline of the thesis

In the present thesis, I investigated biodiversity and different ecological processes involved in forest regeneration. For this purpose, I conducted three studies in a fragmented mosaic-forest landscape in KwaZulu-Natal, South Africa. In particular, I compared seed predation by rodents, establishment of woody seedlings and saplings, and leaf damage of woody seedlings and saplings by insects and pathogens between scarp forest fragments embedded in variable matrix habitat.

The mosaic landscape of southeast KwaZulu-Natal is especially suitable for such comparisons, as it was characterized by scarp forest fragments within natural grassland matrix before the expansion of agricultural land (Cooper 1985). Due to ongoing deforestation, the scarp forest cover has significantly declined (Eeley *et al.* 2001). Nowadays, undisturbed fragments are confined to nature reserves, whereas fragments that endured human land-use changes remained within modified agricultural surroundings, such as sugarcane fields and eucalypt plantations. Remaining fragments are of high conservation value as a result of their high biodiversity and degree of endemism (Eeley *et al.* 2001; von Maltitz *et al.* 2003). In this landscape mosaic, I established 24 study plots within selected scarp forest fragments that were surrounded by four different matrix habitat types. Study plots within large forest fragments featuring natural forest matrix and small forest fragments enclosed by natural grassland matrix habitat were located within Vernon Crookes and Oribi Gorge nature reserves. Small fragments with modified matrix habitat were in close distance to these nature reserves and situated within sugarcane fields and eucalypt plantations.

The aims of my thesis were to quantify the impact of structural forest fragment quality and variable matrix habitat surrounding forest fragments on 1) rodent seed predators and seed predation, on 2) tree diversity and establishment of woody seedlings and saplings, and on 3) arthropod herbivore and predator abundances as well as on insect herbivory and leaf fungal pathogen infestation of woody seedlings and saplings. Consistent with these aims, my thesis is composed of three major chapters (2, 3, 4). They are framed by a general introduction (chapter 1) at the beginning as well as general conclusions (chapter 5) and future challenges (chapter 6) at the end. A German summary can be found at the very end (chapter 7). The three main chapters are structured like scientific journal publications starting with an abstract, followed by an introduction, a methods section, the presentation of results, their discussion and deductible conclusions. They can therefore be read as independent units. Please, note that this has led to redundancy of some of the content.

Chapter 2 is concerned with the influence of forest fragment quality and matrix habitat on the rodent seed predator community and the process of seed predation. Therefore, I assessed ground vegetation cover as an important structural characteristic for rodents, rodent abundance, species richness and community composition as well as seed predation in scarp forest fragments surrounded by variable matrix habitat.

In chapter 3, I investigated the impact of forest fragment quality and matrix habitat on woody seedling and sapling establishment. To do so, I considered canopy cover, light intensity and vegetation complexity for species richness, abundance and community composition of trees, seedlings and saplings in scarp forest fragments surrounded by variable matrix habitat. Moreover, I differentiated between early- and late-successional species and separately analyzed tree recruits originated from external seed influx between forest fragments with variable matrix habitat.

Chapter 4 deals with the consequences of forest fragment quality and matrix habitat for arthropods as well as for leaf damage of woody seedlings and saplings. I quantified the effect of structural components of fragments, *i.e.* tree diversity, vegetation complexity and canopy cover as well as of matrix habitat on the arthropod predator and herbivore community as well as on insect herbivory and leaf fungal pathogen infestation of tree recruits.

2 Elevated seed predation in small forest fragments embedded in high-contrast matrices

With Lena Fischer, Eike Lena Neuschulz, Colleen T. Downs and Nina Farwig

Abstract. Anthropogenic forest fragmentation has been hypothesized to increase levels of seed predation *via* elevated rodent abundances, thus affecting forest regeneration. We tested this prediction by investigating the consequences of forest fragment quality in terms of structural characteristics and matrix habitat on rodent communities and seed predation in KwaZulu-Natal, South Africa. We estimated herbal ground vegetation cover as a measure of forest fragment quality relevant for rodents. We compared rodent abundance, species richness and community composition as well as seed predation between large scarp forest fragments with natural forest matrix and three small forest fragments surrounded by natural grassland, eucalypt plantations and sugarcane agriculture. We assessed rodent communities using pitfall traps, drift fences and live traps. We quantified seed predation by placing peanuts inside and outside rodent exclosures. Rodents were important seed predators in all small fragments. Rodent abundance and species richness as well as seed predation were higher in small forest fragments than in large fragments, but significantly higher only in fragments surrounded by agriculture. Forest fragment quality by means of higher ground vegetation cover enhanced rodent abundance and richness as well as seed predation pressure in small forest fragments. Possibly, the high-contrast sugarcane matrix posed a barrier to top predators resulting in the ecological release of rodents in these forest fragments. Additional studies are needed to determine whether increased seed predation in small forest fragments reduces seed survival and consequently regeneration.

Key words. Bottom-up processes, forest fragmentation, forest regeneration, habitat quality, human impact, KwaZulu-Natal, plant-animal interactions, rodents, scarp forest.

Introduction

Seed predation is a critical determinant of seed survival, seedling establishment and ultimately forest regeneration (Stoner *et al.* 2007; Farwig *et al.* 2008a). Particularly rodents have been shown to play an important role in the complex multi-step process of forest regeneration (Wang & Smith 2002; Jansen *et al.* 2004). For instance, Cole (2009) has shown that rodents are main seed predators in forest fragments exceeding predation rates of insects or fungal pathogens. Furthermore, Tallmon *et al.* (2003) reported a clear relationship between forest fragmentation, elevated rodent abundances and seed predation. Thus, it has been hypothesized that forest fragmentation increases the levels of seed predation by rodents to the point that the regeneration potential is affected (Asquith *et al.* 1997).

Forest fragmentation causes altered microclimatic and light conditions, which can affect bottom-up processes (Hunter & Price 1992) and might entail changes of vegetation structure (Saunders *et al.* 1991). This can in turn enhance forest the fragment quality for rodents by creating more favourable conditions, as they prefer well-developed understory vegetation with a complex selection of microhabitats and protection from predators (Hay & Fuller 1981; Hagenah *et al.* 2009). Accordingly, a decrease in ground vegetation cover has been shown to lead to a decline in rodent species diversity in intensively logged forests in Kenya (Mortelliti & Boitani 2006). In addition, top-down processes can be affected through forest fragmentation (Terborgh *et al.* 2008) and the loss of rodent predators might in turn lead to the ecological release of rodent communities (Hunter & Price 1992). Elevated rodent abundances often result in increased seed predation pressure in small forest fragments (Donoso *et al.* 2003; García & Chacoff 2007) and consequently influence seedling establishment (Asquith *et al.* 1997).

Not only changes in rodent abundance, but also in rodent species richness and community composition might influence seed predation patterns in fragmented forests. Rodent species differ in their preferential nutrient sources (Wirminghaus & Perrin 1992) and therefore also in their effect on overall seed predation. Thus, the impact of forest fragmentation on rodent seed predation might strongly depend on the community composition of seed predators. Despite these ambiguous patterns, rodent community responses and seed predation have only rarely been studied simultaneously in the face of forest fragmentation (but see

Lambert *et al.* 2005; Farwig *et al.* 2008a; Cordeiro *et al.* 2009). Especially in Africa, where an extensive human population growth is expected (Wright & Muller-Landau 2006) and human impact on forests is already severe, the influence of fragmentation on seed predation and ultimately regeneration processes is poorly understood.

Forest fragmentation is largely driven by conversion of natural forests to cultivated land including agriculture, such as cereals or sugarcane and plantations, *e.g.* eucalypt for timber (MEA 2005). Thus, cultivated matrices play an important part in fragmented landscapes and are of high relevance for biodiversity and interspecific interactions (Prevedello & Vieira 2010). The effects of matrices surrounding forest fragments might even prevail over isolation and exceed fragmentation effects, such as reduced area and creation of edges (Kupfer *et al.* 2006). The matrix type surrounding fragments of remaining forest and its permeability matter in the context of landscape connectivity, corridors and stepping stones (Ricketts 2001; Haila 2002; Kupfer *et al.* 2006). This can have consequences for rodents, for which different matrices of high or low contrast to the remaining forests might be more or less beneficial in terms of resources or shelter. Additionally, this might also be true for rodent predators and might therefore *via* top-down control influence rodent communities (Hunter & Price 1992).

In view of that, these possible matrix effects on rodents can in turn affect seed predation (Farwig *et al.* 2009). Herrera *et al.* (2011) for example found that seed predation can be higher in unconnected patches than in fragments that are connected by forested areas. Consequently, the need to take the matrix into account when studying forest fragmentation and consider the entire landscape mosaic has been expressed widely (*e.g.* Daily *et al.* 2003; Bennett *et al.* 2006; Vandermeer & Perfecto 2007). However, none of the few studies investigating rodent communities and seed predation has focused on effects of both forest fragment quality and the matrix habitat surrounding remaining forest fragments.

We studied the influence of fragment quality and matrix habitat on rodent communities and on seed predation. We compared abundance, species richness and community composition of rodents as well as seed predation between large natural scarp forest fragments with forest matrix and three small scarp forest fragment types surrounded by natural grassland, eucalypt plantations and sugarcane agriculture in KwaZulu-Natal, South Africa. We hypothesized (1) rodents to be the main drivers of seed predation and accordingly that an increase of rodents leads to higher seed predation and (2) rodent abundance, species richness and community composition as well as seed predation to be

differently affected by forest fragment quality and matrix habitat. This might be due to changes in ground vegetation cover and the varying permeability and resource availability of surrounding matrices for rodents as well as rodent predators. Specifically, we predicted rodent abundance, species richness and seed predation to be lowest in large natural forest fragments with forest matrix, low in forest fragments surrounded by natural grassland, intermediate in fragments surrounded by eucalypt plantations and highest in fragments surrounded by sugarcane agriculture.

Methods

STUDY AREA AND DESIGN. Field work was conducted between November 2008 and mid February 2009 in coastal scarp forest of 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 (Fig. 2.1a). Scarp forest forms a transition zone between Afromontane forest and Indian Ocean coastal belt forest. It is located on south- and southeast-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 (Lawes 1990; Eeley *et al.* 1999). They belong to the summer rainfall (October–March) subtropical climate zone and feature seasonal differences with an annual temperature range from 4 to 32°C and a rainfall range from 440 to 1400 mm (von Maltitz *et al.* 2003). The rainy season in 2008 started in November. Hence, during our study period food resources were low on the ground for the rodents in all forest fragments as most fruits were still in the trees.

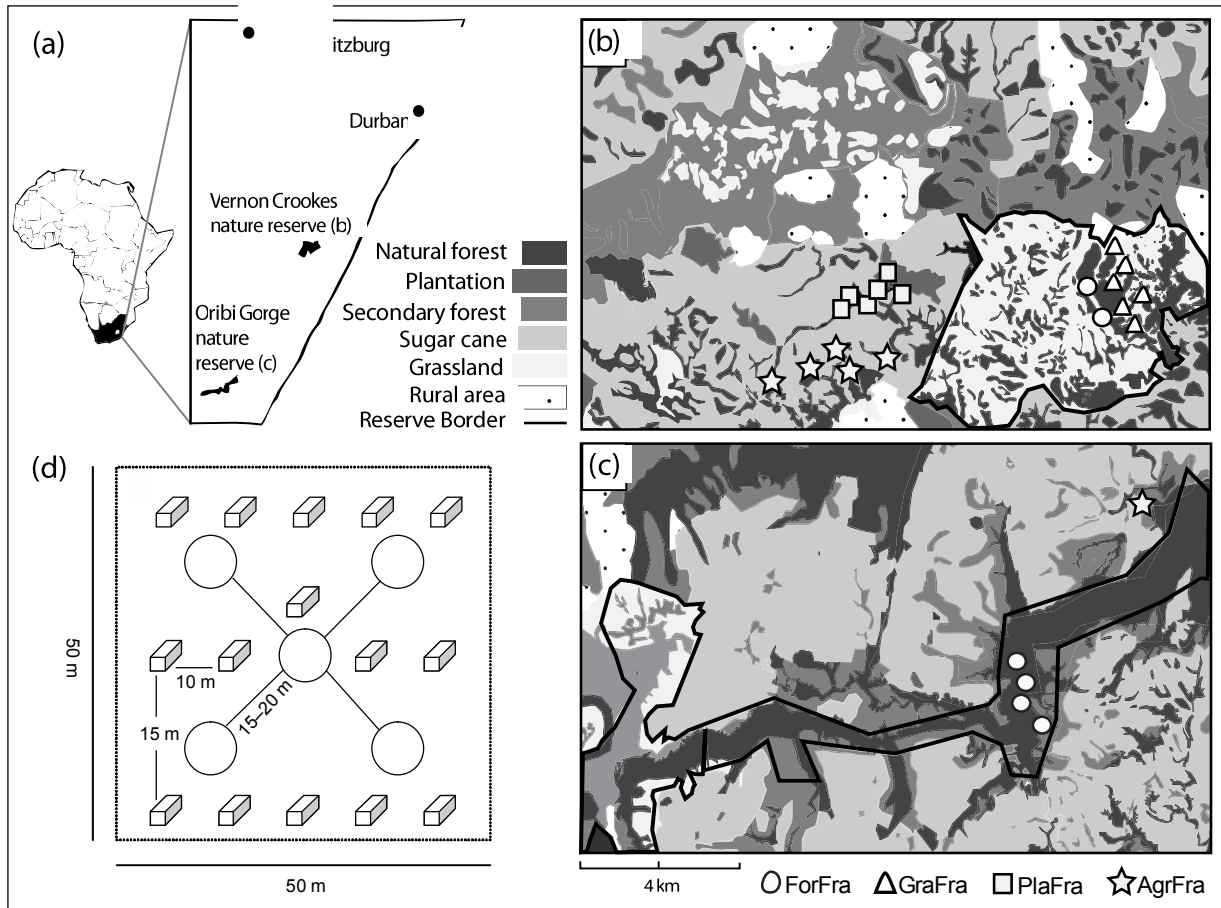


Figure 2.1. Study area and research design. (a) Map of South Africa (black) and detailed map of study area. Landscapes around (b) Vernon Crookes and (c) Oribi Gorge nature reserves showing the 24 study plots with six each in large natural forest fragments with forest matrix (ForFra; circles) and three small forest fragment types surrounded by natural grassland (GraFra; triangles), plantation (PlaFra; squares) and agriculture (AgrFra; stars) matrix habitat. (d) Research design for assessing rodent communities and seed predation illustrating the arrangement of pitfall traps (circles) and drift fences (lines between circles), live traps (rectangles) and seed stations (circles).

We studied scarp forest fragments surrounded by four variable matrix habitat types, *i.e.* two natural heterogeneous matrices within the two nature reserves and two modified homogenous matrix habitat types located outside the nature reserves. Forest fragments in natural matrix habitat were: (1) large natural forest fragments with forest matrix (ForFra; within two forest blocks) and (2) small forest fragments surrounded by natural grassland containing isolated trees and bushes (GraFra) kept open due to microclimatic conditions, grazing pressure and fire events. Small fragments in modified matrix habitat comprised: (1) forest fragments enclosed by plantations (PlaFra) consisting of small remnant stretches of native forest as buffer zones of nearby streams within eucalypt plantations (major timber of the region) and (2) forest fragments surrounded by sugarcane agriculture (AgrFra; major crop of the region). All forest fragment types enclosed by variable matrix habitat differed in

environmental characteristics, such as size, canopy cover, ground vegetation cover and altitudinal range (Table 2.1).

Table 2.1. Forest fragment type characteristics. Given are means \pm 1SE except for sizes of large forest fragments with forest matrix (ForFra), which are the total forest block sizes. GraFra = small fragments surrounded by natural grassland; PlaFra = small fragments surrounded by plantations; AgrFra = small fragments surrounded by agriculture; VC = Vernon Crookes nature reserve; OG = Oribi Gorge nature reserve; veg. = vegetation; asl = above sea level.

Forest fragment type	Mean size (ha)	Mean canopy cover (%)	Mean ground veg. cover (%)	Altitudinal range (m asl)
ForFra	VC: 130	92.5 \pm 4.2	6.7 \pm 3.3	220–390
	OG: 822			
GraFra	2.3 \pm 0.9	77.5 \pm 10.6	24.2 \pm 11.3	340–480
PlaFra	0.6 \pm 0.3	82.5 \pm 5.6	55.0 \pm 9.1	480–510
AgrFra	3.2 \pm 0.7	91.7 \pm 8.3	62.5 \pm 5.0	390–580

We established a total of 24 study plots, *i.e.* six replicates of 50 \times 50-m plots per fragment type (Fig. 2.1b, c). Minimal distance between plots was 500 m except for PlaFra, which were at least 200 m apart. Because the different fragment types were not evenly distributed throughout the two study regions, replicates of most fragment types were spatially clustered (Fig. 2.1b, c). However, both regions lie within the natural distribution range of scarp forest and thus experience very comparable topographic, soil and climatic conditions, such as sandstone, orographic rainfall and strong winds (von Maltitz *et al.* 2003). Moreover, they feature a similar tree species composition. The most dominant tree species in ForFra, *i.e.* *Baphia racemosa*, *Englerophytum natalense* and *Millettia grandis* are equally abundant in both regions (see Appendix 2). Additionally, both regions are exposed to comparable land-use modifications (sugarcane fields, timber plantations).

RODENT SAMPLING. To assess rodent communities we set up five pitfall traps connected by drift fences (Umetsu *et al.* 2006) in all fragment types. Pitfall traps (plastic buckets of 25-L volume, 42-cm diameter at the top, 45-cm depth with small holes at the bottom to provide drainage) were located at five points within the plot: one in the centre of the 50 \times 50-m plot and four in the middle of four 25 \times 25-m subsquares of the plot (Fig. 2.1d, circles). Drift fences (80% dark-green shade cloth, 50 cm high) were spanned diagonally from the outer

traps towards the central pitfall trap (15–20 m length) and were tightly attached to the ground. Further, 15 non-folding Sherman live traps (25.4 × 7.6 × 7.6 cm) were set up in rows of five traps each with a minimum distance of 10 m separating them (Fig. 2.1d). We used a mixture of peanut butter and oats as bait. Trapping was conducted for three consecutive days on three plots of different fragment types that were chosen randomly. We checked traps in the early morning and late afternoon to account for diurnal animals as well. To avoid double counting, we semi-permanently marked rodents inconspicuously with dark-green spray colour (Aerolak, Plascon) on their lower side to prevent increased detectability by predators. We identified captured animals with two field guides (Smithers 2000; Stuart & Stuart 2007) and weighed and measured them using a calliper and spring balance. Afterwards we released them directly on site. We determined: (1) abundance as mean number of individuals per plot, (2) species richness as mean number of species per plot, and (3) α -, β_1 - and β_2 -diversity, whereby β -diversity was used as a proxy for differences in community composition (see data analyses for details). One replicate of GraFra was lost due to flooding leaving 23 plots for analyses.

SEED PREDATION. To quantify seed predation pressure, we placed non-germinable half peanuts (one cotyledon) on paper dishes (diameter 18 cm) at five stations per plot (same locations as pitfall traps, Fig. 2.1d, circles). We are aware of possible problems fraught with offering non-naturally occurring seeds. For instance, there might be differences in the behaviour of different rodent species when offered a novel food source. However, as we applied the same experimental design to all study plots, comparisons among the forest fragment types are valid in a relative sense. Moreover, as no natural seeds were available, we can exclude the effect of potential dietary preferences of different rodent species. Time of sampling was randomized among fragment types. To be able to separate vertebrate from invertebrate seed predation, we offered ten seeds on open dishes (= open treatment), accessible to all predators as well as ten seeds within cubic, closed-topped mesh wire enclosures (20 × 20 × 20 cm, 1.2-cm mesh width), which excluded vertebrate predators (= enclosure treatment). Seeds were placed in the late afternoon and checked the following three mornings. We counted depredated seeds (= removed or more than half eaten) and replaced them on each plate. Rodents are known to often scatter-hoard rather than depredate seeds that they remove in other forest systems (Jansen *et al.* 2006; Forget & Cuiljpers 2008).

However, we found no evidence for secondary seed dispersal in our study sites. There was no proof of scatter-hoarding and the few recorded dispersal events were of extremely short distance (*i.e.* < 1 m; data not shown). We thus assumed that seed removal equalled seed predation in our trials. Our estimate for rodent seed predation pressure was the mean difference of depredated seeds per day and plot between open and enclosure treatments (hereafter seed predation). Seed stations were lost for one replicate of AgrFra due to disturbance by monkeys leaving 23 plots for analyses.

FOREST FRAGMENT QUALITY. At each site, we assessed herbaceous ground vegetation cover at the height of 20 cm as a measure of forest fragment quality for rodents. We estimated the percentage of ground cover at five 5 × 5-m squares in each plot approximately where pitfall traps and seed stations had been located and calculated means per plot (Table 2.1).

DATA ANALYSES. We used EstimateS (Colwell 2009) to estimate overall rodent species richness of the pooled samples of the different fragment types after 100 randomizations of sample order (Gotelli & Colwell 2001). We used three non-parametric species richness estimators: the abundance-based coverage estimator ACE, the Chao 2 estimator, and the second-order Jackknife estimator Jack 2. The latter two are based on presence/absence data of species occurring in only one or two samples (Chao 2005). We chose Chao 2 and Jack 2 as they are the least-biased estimators for small sample sizes (Colwell & Coddington 1994). We further used the abundance-based estimator ACE because for most captured species, we encountered fewer than ten individuals.

To analyse diversity of rodents we followed an additive partitioning approach and used the total number of rodent species obtained in the three days of sampling. Additive partitioning has been described as a straightforward method that allows a direct comparison of the single diversity components (α and β) that contribute to total observed diversity (γ_{obs}) over several spatial scales, as they all have the same unit (Crist *et al.* 2003; Clough *et al.* 2007). We additively partitioned rodent diversity for each fragment type as:

$$\chi_{\text{obs}} = \alpha + \beta_1 + \beta_2$$

where α is the mean number of species of each fragment type, *i.e.* it is the same as our species richness and thus will be discussed as that separately; β_1 is the species turnover between replicates of one fragment type and is obtained by subtracting α from γ_1 , the total number of species of that fragment type; and β_2 is the species turnover among the different fragment types and results from subtracting γ_1 from γ_2 , the total number of species of all samples (Crist *et al.* 2003; Clough *et al.* 2007). We used β_1 as a measure for variability of rodent community composition within replicates of one fragment type and β_2 as a proxy for differences in community composition among fragment types. β is a measure of dissimilarity: the higher β , the less species were shared between the different replicates of one fragment type or among the different fragment types.

We used analyses of covariance (ANCOVA) to test for effects of forest fragment quality (*i.e.* ground vegetation cover) and the four forest fragment types surrounded by variable matrix habitat (ForFra, GraFra, PlaFra, AgrFra) on rodent abundance and species richness as well as on seed predation. Rodent abundance and species richness were square root-transformed to reach homogeneity of variances and normality of residuals. Rodent abundance was included into the model testing for effects of fragment type on species richness as species richness might increase with abundance (Gotelli & Colwell 2001). We also included rodent abundance as a covariate into the model testing for effects of fragment type on seed predation to control for differences in numbers of rodent individuals. Moreover, we incorporated altitude as a covariate into the models to control for altitudinal differences between fragment types as well as location (VC or OG) to control for clustering of fragment types within study regions. Independent variables were excluded from the models through stepwise deletion starting with the least significant term ($P > 0.05$), which is why the number of degrees of freedom is variable. We tested for differences between ForFra and the small forest fragments using contrasts implemented in Dunnett's *post hoc* test ($P < 0.05$). All analyses were performed with R version 2.12.0 (R Development Core Team 2010).

Results

RODENT COMMUNITY. During a total of 1380 trap nights we caught 25 rodent individuals and seven species (Appendix 1). Trapping success was low with 1.8%. The most commonly captured species was the multimammate mouse *Mastomys* sp. (*M. coucha* and *M. natalensis* cannot be separated in the field (Smithers 2000)) with 14 individuals, whereas the other species were captured with one or two individuals each. None of the seven species was found in all fragment types and four species were found exclusively in one fragment type. No rodents were caught in ForFra (Appendix 1). Most individuals and species were captured in AgrFra (17 individuals, 4 species; Fig. 2.2a, b, α -diversity). Total observed species richness represented between 55 and 84% of the species richness estimated by the three applied estimators (ACE = 8.33, Chao 2 = 8.91 ± 2.78 SD, Jack 2 = 12.74).

Table 2.2. ANCOVA models testing the effects of forest fragment quality matrix habitat on rodent abundance, species richness (both sqrt-transformed) and on seed predation (all $n = 23$) including rodent abundance as a covariate into the species richness model. Given are df-, R^2 -, F - and P -values for full models after stepwise deletion of non-significant (ns) terms and of all model parameters (values just before deletion); * $P < 0.05$, ** $P < 0.01$.

Parameter	Rodent abundance (sqrt)				Species richness (sqrt)				Seed predation			
	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P
Full model	4,18	0.38	4.39	*	5,17	0.45	4.65	**	3,19	0.29	3.96	*
Ground vegetation	1	-	7.08	*	1	-	7.23	*	1	-	1.23	ns
Rodent abundance	-	-	-	-	1	-	6.06	-	1	-	0.41	ns
Matrix habitat	3	-	3.50	*	3	-	3.32	*	3	-	3.96	*

Rodent abundance significantly increased with increasing ground vegetation cover (Table 2.2). It differed significantly between forest fragments with variable matrix habitat (Fig. 2.2a, Table 2.2). Rodent abundance was higher in all small forest fragment types compared to ForFra, but differed significantly only between ForFra and AgrFra (Dunnett's $P = 0.031$). In ForFra we captured no rodent individuals, rodent abundance was low in GraFra (0.80 ± 0.58 ; all reported means are back-transformed if necessary $\pm 1SE$) and PlaFra (0.67 ± 0.42) and highest in AgrFra (2.83 ± 1.40 ; Appendix 1). Rodent abundance was neither

affected by altitude nor location of the different fragment types indicating that clustering of replicates within one fragment type and differences in altitude were unimportant (data not shown).

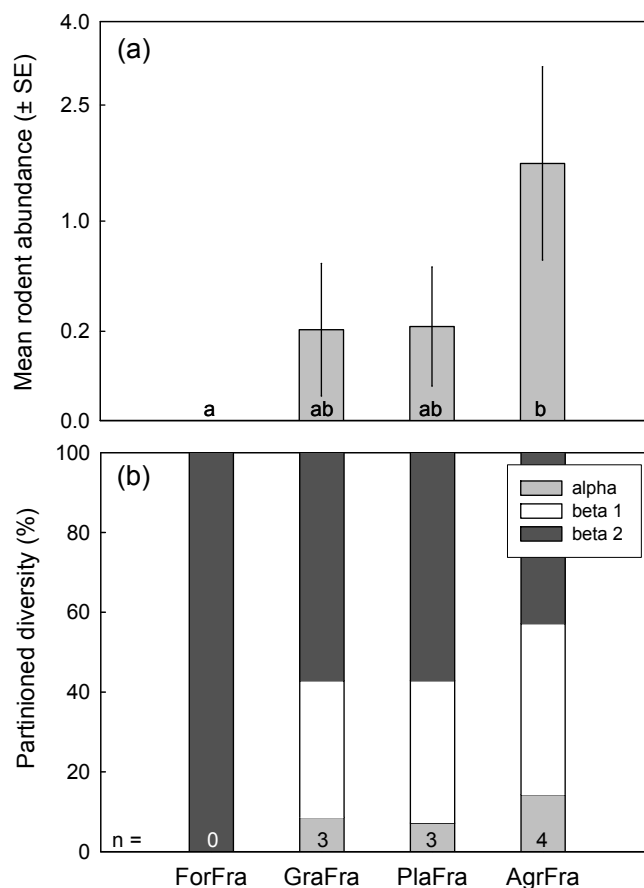


Figure 2.2. Rodent abundance, species richness and composition in forest fragments with variable matrix habitat. (a) Mean (\pm SE) rodent abundance per plot (shown are square root-transformed data). (b) Relative contribution of additively partitioned α - (alpha = species richness), β_1 - (beta 1), and β_2 -diversity (beta 2). ForFra = large natural forest fragments with forest matrix; GraFra = small natural forest fragments surrounded by grassland; PlaFra = small modified forest fragments surrounded by plantations; AgrFra = small modified forest fragments surrounded by agriculture; different letters indicate significant differences between ForFra and small forest fragments according to Dunnett's *post hoc* test, $P < 0.05$.

Rodent species richness significantly increased with ground vegetation cover (Table 2.2). It also differed significantly between forest fragments surrounded by variable matrices (Fig. 2.2b, α -diversity, Table 2.2). All small forest fragments had a higher rodent species richness than ForFra, but merely in AgrFra richness tended to be higher than in ForFra (Dunnett's $P = 0.058$). In ForFra we found no species, in GraFra and PlaFra species numbers were low (0.60 ± 0.40 , $\alpha = 8.6\%$; 0.50 ± 0.34 , $\alpha = 7.1\%$) and in AgrFra we found comparatively the highest number (1.0 ± 0.89 , $\alpha = 14.3\%$; Appendix 1). Furthermore, species

richness significantly increased with rodent abundance (Table 2.2), but was neither affected by location nor altitude of the fragment types (data not shown).

Partitioned diversity revealed a similar species turnover, *i.e.* composition between replicates (β_1) within all small forest fragment types (range: 34.3–42.9%; Fig. 2.2b, β_1 -diversity). Species turnover among small forest fragments (β_2) ranged from 42.9 to 57.1%, indicating a relatively low share of species and accordingly a diverging community composition among forest fragments surrounded by variable matrix habitat (Fig. 2.2b, β_2 -diversity). However, these differences in rodent community composition were mainly owing to the dominance of one species, *Mastomys* sp.

SEED PREDATION. Rodent feeding scars and droppings in the open seed stations indicated that rodents were important vertebrate seed predators in forest fragments. We also observed slugs and snails as well as insects, such as beetles, ants and flies feeding on the seeds in both treatments in all fragment types. We did not detect bird droppings on the seed stations.

Seed predation, *i.e.* the mean difference of depredated seeds between open and

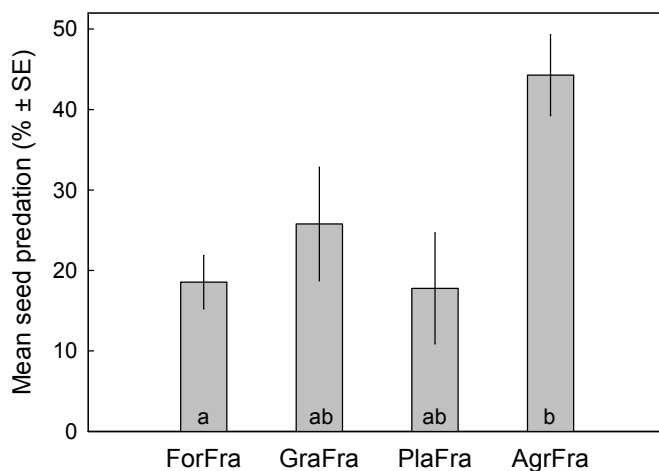


Figure 2.3. Seed predation in forest fragments with variable matrix habitat. Mean (\pm SE) percentage of seed predation. ForFra = large natural forest fragments with forest matrix; GraFra = small natural forest fragments surrounded by grassland; PlaFra = small modified forest fragments surrounded by plantations; AgrFra = small modified forest fragments surrounded by agriculture; different letters indicate significant differences between ForFra and small forest fragments according to Dunnett's *post hoc* test, $P < 0.05$.

enclosed treatments was not significantly affected by ground vegetation cover (Table 2.2). It varied significantly among forest fragments with variable matrix habitat (Fig. 2.3, Table 2.2). Seed predation was significantly higher in AgrFra than in ForFra (Dunnett's $P = 0.020$). It was lowest in ForFra (18.6 % \pm 3.3) and PlaFra (17.8 % \pm 6.9), intermediate in GraFra (25.8% \pm 7.1) and high in AgrFra (44.3% \pm 5.0; Fig 2.3; Appendix 1). Seed predation was not affected by rodent abundance, altitude or region (Table 2.2, data partly shown).

Discussion

Our study shows that rodents were seemingly responsible for seed predation in small forest fragments. The combined effects of forest fragment quality and matrix habitat resulted in increased rodent abundance and species richness, possibly entailing elevated seed predation in small forest fragments compared to ForFra with significant differences between ForFra and forest fragments surrounded by the high-contrast matrix of sugarcane agriculture.

RODENT COMMUNITY. Overall, abundance of rodents was relatively low compared to other tropical and subtropical forests with only a mean number of 1.1 individuals per plot. The number of seven captured species on the other hand was similar to that obtained by others (Wirminghaus & Perrin 1993; Farwig *et al.* 2008a) and represented a high percentage of the estimated richness assessed by two of the three applied richness estimators. Another study on small mammals in Afromontane forests in KZN recorded a slightly higher species richness, but a much higher abundance (Wirminghaus & Perrin 1993). This contrast might be explained by the shorter period of sampling in our study (1380 trap nights *vs.* 7056 trap nights). However, seed predation experiments were straightforward and showed similar or higher predation rates than shown during comparable experimental time frames in other studies (see below; Donoso *et al.* 2003; Farwig *et al.* 2008a). As rodent trapping data coincided with seed predation data in response to the different fragment types, we are convinced that our rodent community data are of informative value, nonetheless. Even though rodent abundance did not significantly influence seed predation pressure, rodents were important seed predators in small forest fragments, as we expected and as has been reported in other studies (Hammond 1995; Notman & Gorchov 2001).

There was considerable variability in community composition among small forest fragments (Appendix 1). However, we captured no rodents in ForFra and therefore cannot make a statement regarding differences between these and small forest fragments. Moreover, differences in community composition were masked by the dominance in abundance of one species, the multimammate mouse, a pattern well-observed in other rodent studies in tropical forests (*e.g.* DeMattia *et al.* 2004; Farwig *et al.* 2008a). Accordingly, rodent abundance

in general was more decisive than community composition for shaping seed predation patterns in small forest fragments.

SEED PREDATION. In line with our hypothesis, we could show increased rodent abundance, species richness and seed predation in small forest fragments compared to ForFra. These findings are in accordance with the results of other studies that also found significantly more rodents and seed predation in modified compared to natural forests (Donoso *et al.* 2003; Farwig *et al.* 2008a; Pardini *et al.* 2009). For instance, Hulme (1998) claimed that the spatial distribution of seed predation can be attributed to the presence of rodents, which is positively influenced by vegetation cover. Furthermore, Gubista *et al.* (1999) found a higher rodent abundance and richness in secondary forest compared to primary forest owing to the structurally diverse understory and mudstone of this forest. In our study AgrFra showed the highest rodent abundance and seed predation and differences to ForFra were most pronounced. In this fragment type ground vegetation was dominated by *Isoglossa woodii*, a herbaceous to semi-woody plant that grows up to 3 m in height (Griffiths *et al.* 2007; Tsvuura *et al.* 2007) creating perfect protection for rodents from predators. We thus assume a cascading effect in AgrFra: increased ground vegetation cover favoured rodents, which presumably caused elevated seed predation. The other two small fragment types, GraFra and PlaFra, showed a similar tendency, which is supported by percentages of ground vegetation cover resembling both rodent abundances as well as seed predation rates in all fragment types (Appendix 1). However, ground vegetation cover neither had a direct influence on seed predation, nor was seed predation significantly affected by rodent abundance in all fragment types. Presumably, this mismatch can mainly be ascribed to the contrasting patterns of rodents (none) and seed predation (intermediate) in ForFra. There, possibly other vertebrate seed predators, too large for the traps, caused the seed predation rates. As squirrels do not occur in our study region, these might have been greater cane-rats (*Thryonomys swinderianus*) or porcupines (*Hystrix africaeaustralis*). Furthermore, due to the lack of undergrowth in ForFra, rodents might have been able to avoid traps. We therefore argue that in small forest fragments the causality that involves ground vegetation cover, rodents and seed predation was direct, whereas in ForFra this was not the case. Thus, rodent communities and seed predation seem to be affected by forest fragment quality causing changes in bottom-up processes, such as biomass production on the ground.

In addition, matrix effects were highly variable, but particularly pronounced for the high-contrast matrix of sugarcane agriculture, as we expected. In this small forest fragment type rodent abundance, species richness and seed predation were significantly higher than in ForFra. This has also been found in fallow agricultural areas compared to mature forest in Peru (Notman & Gorchov 2001). In addition, the agricultural matrix might be avoided by carnivore mammals due to the high frequency of human activities in the fields. The matrix of sugarcane did, however, seemingly not present an obstruction to rodents. Instead, sugarcane rather might have offered an additional food source for rodents. *Mastomys* sp., our most abundant rodent species, even plays an important role as a crop pest in Africa (Stenseth *et al.* 2003). Sugarcane might have also served as a habitat as has been reported by Takele *et al.* (2011) in India who found a high rodent abundance in sugarcane fields.

On the contrary, natural forests and heterogenous grasslands within nature reserves as well as eucalypt plantations might have provided connectivity through low-contrast matrices. Consequently, top predators might have prevented rodents to become overly abundant leading to low seed predation rates there (Terborgh *et al.* 2008). For instance, caracals (*Caracal caracal*) or genets (*Genetta tigrina*) might make use of forests, natural grassland and plantations and thereby control rodent communities (Perrin 2002; Brockerhoff *et al.* 2008; Tofoli *et al.* 2009). Moreover, the fauna in eucalypt plantations might be generally depauperate. Such findings have been shown for a number of taxa in a review on Australian eucalypt plantations (Lindenmayer & Hobbs 2004). Furthermore, a study on bird communities in the same study area also showed low species richness in PlaFra compared to the other forest fragments types (Neuschulz *et al.* 2011). Thus, in spite of the structural similarity to natural forests in terms of canopy cover, eucalypt plantations seem to act as a barrier for the dispersal of rodents and possibly other taxa due to a lack of undergrowth and resources (Bernard *et al.* 2009; Wilson *et al.* 2010). The low percentage of undergrowth might have been an additional reason for the low numbers of rodents in GraFra as these were structurally very similar to ForFra.

Conclusions

In consequence, our study shows that forest fragment quality in terms of ground vegetation cover and matrix habitat influenced rodent communities and seed predation. In small scarp

forest fragments with high ground vegetation cover and high-contrast matrices rodents might be favoured by bottom-up processes regarding resources and shelter as well as seemingly by top-down processes, such as the absence of predators. Consequently, elevated seed predation pressure might impede seed survival, lead to a decline in seedling establishment and ultimately affect regeneration within these scarp forest fragments. However, further studies need to verify whether establishment of seedlings and saplings is considerably hampered in small scarp forest fragments.

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3 Late-successional tree recruits decrease in forest fragments with modified matrix habitat

With Lena Fischer and Nina Farwig

Abstract. Conversion of natural ecosystems has increased the proportion of fragmented forests worldwide. Long-term regeneration dynamics of forest fragments depend on the availability of seeds, seedlings and saplings. We therefore assessed the influence of forest fragment quality regarding structural characteristics and matrix habitat on natural recruitment in KwaZulu-Natal, South Africa. We determined forest fragment quality in terms of canopy cover, relative light intensity and vegetation complexity, which are crucial parameters for tree recruitment. We compared species richness, abundance and composition of trees, woody seedlings and saplings between scarp forest fragments with variable matrix habitat, *i.e.* two natural heterogenous and two modified homogenous matrices. Forest fragments within natural matrices included large fragments with forest matrix and small fragments surrounded by grassland; small forest fragments with modified matrices were embedded in eucalypt plantations and sugarcane agriculture. We categorized all stage classes according to their successional status as either early- or late-successional. Recruitment was further differentiated as originating from external seed influx if no conspecific adult tree was present within the plot. Tree communities were impacted in fragments surrounded by plantations, which comprised lower richness and abundance of late-successional species. In fragments enclosed by modified matrices both richness and abundance of early-successional seedlings and saplings proliferated at the expense of late-successional species, which was confirmed by community composition analysis. These compositional changes in fragments with modified matrices might have been caused by decreased forest fragment quality, such as lower canopy cover and higher light intensity. Matrices presumably did not act as strong barriers for animal-mediated seed influx as external recruitment occurred in all fragment types. These findings demonstrate that regeneration seems to be hampered by joint effects of forest fragment quality and matrix habitat. Yet, existing seed influx across the structurally complex landscape highlights the importance of forest fragments as stepping-stones.

Key words. Forest fragmentation, forest regeneration, habitat quality, human impact, KwaZulu-Natal, saplings, seed influx, seedling establishment, successional status.

Introduction

Anthropogenic activities entailing an annual deforestation rate of 13 million ha (FAO 2010) have led to a growing interest in the regeneration dynamics of fragmented forests. Successful forest regeneration is based on several ecosystem processes along different stages in the life-cycle of trees (Wang & Smith 2002). For instance, most tropical and subtropical tree species depend on pollination and active seed dispersal by animals to permit seedling and sapling establishment and consequently forest regeneration (Howe & Smallwood 1982; Stoner *et al.* 2007). Seed dispersal ensures the transportation of seeds away from the mother plant where seedling establishment is more likely to be successful (Janzen 1970; Connell 1971). In forest fragments seed disperser communities might be impoverished (Cordeiro & Howe 2001). This might result in an increase of seedling establishment near adult conspecifics where competition among siblings is high and the offspring is more susceptible to species-specific herbivores and pathogens (Janzen 1970; Connell 1971). In the long term this may reduce tree diversity (Wright & Duber 2001) as regeneration relies on the availability of recruits and their ability to survive and establish (Martínez-Ramos & Soto-Castro 1993; Benítez-Malvido & Martínez-Ramos 2003a). Assessing seedling and sapling establishment reveals insights into the regeneration potential of fragmented forests (Babaasa *et al.* 2004).

Forest fragmentation changes abiotic factors leading to edge effects, such as modified canopy cover, light intensity and vegetation structure (Saunders *et al.* 1991; Murcia 1995; Montgomery & Chazdon 2001; Harvey *et al.* 2006). These alterations of forest fragment quality can have negative consequences, *e.g.* diminished seedling species richness, loss of rare species and reduced seedling abundance in small forest fragments with many edges (Benítez-Malvido 1998; Benítez-Malvido & Martínez-Ramos 2003b). In addition to abiotic factors, biotic interactions can influence recruitment indirectly. For instance, gaps in the canopy that favour dominant species in the understory of forests have been shown to hinder seedling establishment through interspecific competition (Griffiths *et al.* 2007). Their cover increases herbivory on seedlings by providing shelter and habitat to herbivores on the ground (Lei *et al.* 2002). Furthermore, predator movement is potentially hampered in fragmented forests, which can result in enlarged seed predator and herbivore communities diminishing seed availability and seedling establishment (Terborgh *et al.* 2008).

Conclusions on the impact of forest fragmentation on regeneration processes are not simple. Even though changes may not be susceptible at the species richness and abundance level species composition may be strongly impacted in fragmented forests (Chazdon 2003). Accordingly, species richness and abundance are not always the most suitable indicators for changes in forest regeneration dynamics. Several studies have found a compositional shift in successional status, such as early- and late-successional species in forest fragments (Cordeiro & Howe 2001; Benítez-Malvido & Martínez-Ramos 2003a; Farwig *et al.* 2008b). One explanation is that higher light intensity near edges favours early-successional species and results in a decline of late-successional species (Laurance *et al.* 2006). It is therefore necessary to consider changes of community composition and successional status to understand fragmentation effects on forest regeneration dynamics.

Besides abiotic and biotic changes within forest fragments also the surrounding matrix influences tree communities (Nascimento *et al.* 2006). Depending on structure and permeability, matrices can on the one hand complement natural habitat, facilitate dispersal among habitat remnants and buffer negative effects of forest fragmentation. On the other hand they might as well function as ecological species traps or source of invasive species (Kupfer *et al.* 2006; Brockerhoff *et al.* 2008 and references therein). Thus, low-contrast matrices composed of diverse, structurally complex landscapes that resemble the natural habitat, might aid regeneration (Herrera & García 2009). They might permit movement of seed dispersers and thereby contribute to the stability of anthropogenically modified landscapes (Tewksbury *et al.* 2002). For instance, Estrada and Coates-Estrada (2001) showed a higher abundance of seed-dispersing bats in forest fragments surrounded by cacao or coffee plantations than in fragments surrounded by pastures. On the contrary, high-contrast matrices comprising homogenous, structurally poor elements might have the opposite effect and hamper species movement and plant-animal interactions (Tewksbury *et al.* 2002). In this regard, external recruitment originating from seed influx can be used as an indicator of seed dispersal in forest fragments (Martínez-Ramos & Soto-Castro 1993; Melo *et al.* 2010) and can thus be useful to evaluate matrix quality and permeability for seed-dispersing animals. To our knowledge, previous studies regarding human impact on establishment of tree recruits have rarely considered the role of matrix habitat of fragmented forests (but see Nascimento *et al.* 2006).

We studied the effects of forest fragment quality and matrix habitat on tree communities and natural recruitment in KwaZulu-Natal, South Africa. We quantified the role of forest fragment quality considering canopy cover, relative light intensity and vertical vegetation complexity for trees and woody seedlings and saplings. We further compared species richness, abundance and community composition of the three stage classes between forest fragments with variable matrices: two fragment types with natural heterogeneous matrices as well as two fragment types with modified homogeneous matrices. We classified species according to their successional status as either early- or late-successional. Additionally, we considered seedlings and saplings as external recruits if respective adults were missing within the same plot. We expected (1) richness and abundance of early-successional species of all stage classes to be higher in forest fragments with modified matrix habitat and of late-successional species to be higher in fragments with natural matrices, (2) a compositional shift towards more early-successional species in fragments with modified matrices, and (3) abundance of external recruits of animal-dispersed species to be lower in forest fragments with modified matrices due to their possibly reduced permeability for seed dispersers.

Methods

STUDY AREA AND DESIGN. 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'E) and Oribi Gorge (OG; 30°41'S–30°45'S, 30°10'E–30°18.5'E) nature reserves (Fig. 3.1a). Scarp forest forms a transition zone between Afromontane forest and Indian Ocean coastal belt forest. It is located on the south- and southeast-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. As a consequence, scarp forests contain much of the region's biodiversity (Lawes 1990; Eeley *et al.* 1999). They belong to the summer rainfall (October–March) subtropical climate zone and feature seasonal differences with an annual temperature range from 4 to 32°C and a rainfall range from 440 to 1400 mm (von Maltitz *et al.* 2003).

We studied scarp forest fragments surrounded by four variable matrix habitat types, *i.e.* two heterogeneous natural matrices within the two nature reserves and two homogeneous

modified matrix habitat types located outside the nature reserves. Forest fragments in natural matrix habitat were: (1) large natural forest fragments with forest matrix (ForFra) within two forest blocks (total size: VC 130 ha, OG 822 ha, altitudinal range: 220–390 m asl) and (2) small forest fragments surrounded by natural grassland containing isolated trees and bushes (GraFra) kept open due to microclimatic conditions, grazing pressure and fire events (size: 2.3 ± 0.9 ha, all reported means are ± 1 SE; altitudinal range: 340–480 m asl). Small fragments in modified matrix habitat comprised: (1) forest fragments embedded in plantations (PlaFra) consisting of small remnant stretches of native forest as buffer zones of nearby streams within eucalypt plantations (major timber of the region, size: 0.6 ± 0.3 ha, altitudinal range: 480–510 m asl) and (2) forest fragments enclosed by agriculture (AgrFra), *i.e.* large sugarcane fields (predominant crop of the region, size: 3.2 ± 0.7 ha, altitudinal range: 390–580 m asl).

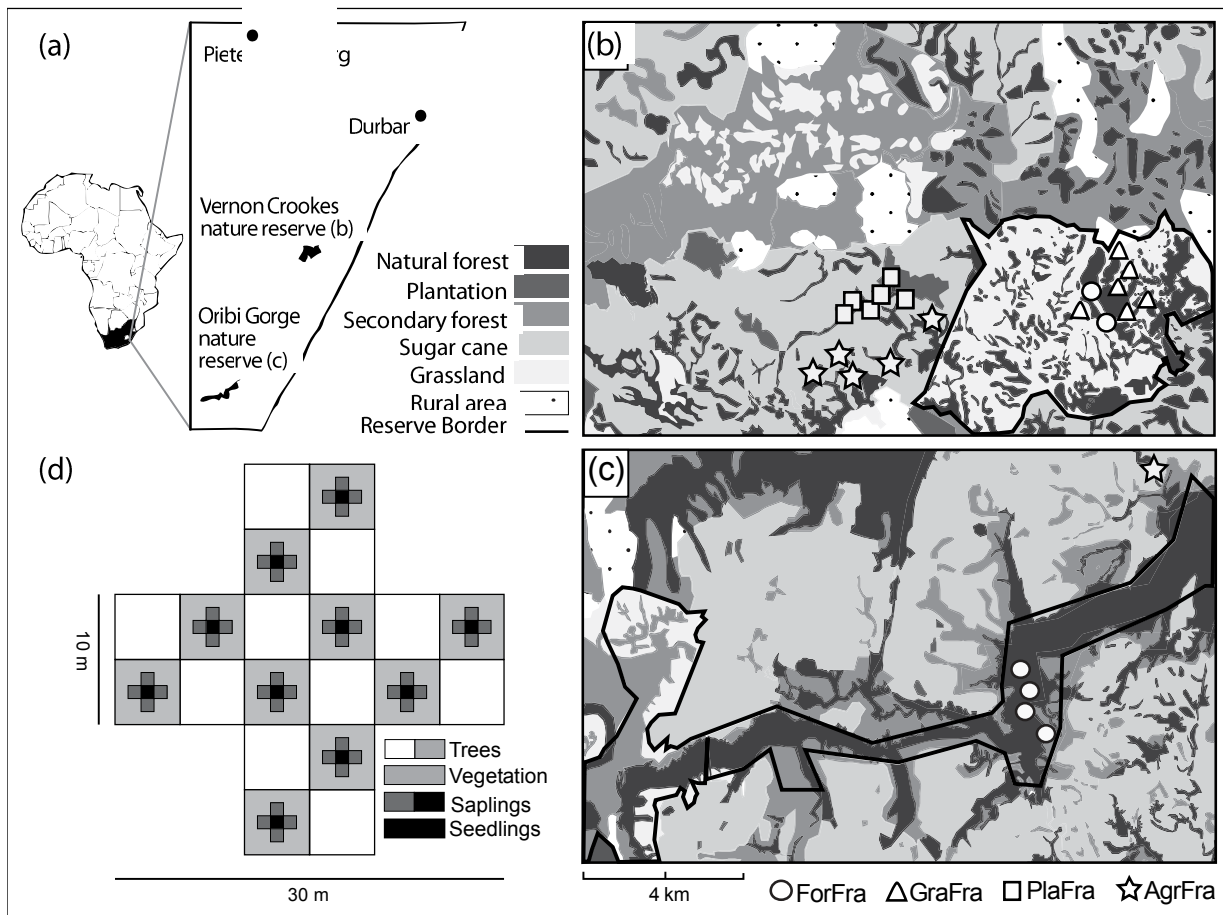


Figure 3.1. Study area and research design. (a) Map of South Africa (black) and detailed map of study area. Landscapes around (b) Vernon Crookes and (c) Oribi Gorge nature reserves showing the 24 study plots with six each in large natural forest fragments with forest matrix (ForFra; circles) and in three small forest fragment types surrounded by natural grassland (GraFra; triangles), plantation (PlaFra; squares) and agriculture (AgrFra; stars) matrix habitat. (d) Research design for assessing tree, seedling and sapling communities as well as vegetation parameters.

We established a total of 24 study plots, *i.e.* six plots per fragment type surrounded by variable matrix habitat (Fig. 3.1b, c). Minimal distance between plots was 500 m except for PlaFra, which were at least 200 m apart. Because the different fragment types were not evenly distributed throughout the two study regions, replicates of most fragment types were spatially clustered (Fig. 3.1b, c). However, both regions lie within the natural distribution range of scarp forest and thus experience very comparable topographic, soil and climatic conditions, such as sandstone, orographic rainfall and strong winds (von Maltitz *et al.* 2003). Moreover, they feature a similar tree species composition. The most dominant tree species in ForFra, *i.e.* *Baphia racemosa*, *Englerophytum natalense* and *Millettia grandis* are equally abundant in both regions (see Appendix 2). Additionally, both regions are exposed to comparable land-use modifications (sugarcane fields, timber plantations).

TREE, SEEDLING AND SAPLING MAPPING. We identified all adult trees with a diameter at breast height (dbh) of > 5 cm or > 400 cm high on a cross of two 30 × 10-m transects (500 m²) per plot. This transect was divided into 20 5 × 5-m subplots (Fig. 3.1d). In every second of these subplots we established ten 5-m² sapling plots (50 m²) to sample all saplings with a diameter of < 5 cm at their base or > 75 cm high. In the centre of these sapling plots we mapped all seedlings with a diameter of < 1 cm at their base or < 75 cm high on ten 1-m² seedling plots (10 m²). Species were identified using Boon (2010), van Wyk and van Wyk (2007) and Coates Palgrave (2005; Appendix 2); species nomenclature follows Coates Palgrave (2005). Species were classified according to their successional status as early- (ES) or late-successional (LS) species depending on their ability to cope with shade following two expert botanists from KZN, Tony Abbott and David Johnson (pers. comm.; Appendix 2). Species that occurred in open woodland or at river margins as well as invasive species were classified as ES.

FOREST FRAGMENT QUALITY. As parameters of forest fragment quality relevant for the establishment of tree recruits, we quantified canopy cover, relative light intensity on the forest floor and vertical vegetation complexity. In the same alternating ten 5 × 5-m subplots within the cross transect described above we estimated percentage of canopy cover at two points directly adjacent to the ten sapling plots using a sighting tube (4 × 10 cm) and averaged estimations across plots. We also measured light intensity always at noon on the

forest floor at the centre of each of the ten 1-m² seedling plots applying a luxmeter (ATP, LX-332). We additionally measured a reference light intensity at an unshaded spot nearby and calculated mean relative light intensity (hereafter light intensity) per plot. Furthermore, we estimated the vertical vegetation complexity (vegetation complexity) to characterize plots according to their vegetation structure (Fig. 3.1d, vegetation). 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 H , to calculate vegetation complexity as suggested by Bibby *et al.* (2000) at each of the ten subplots and averaged values per plot.

RECRUITMENT WITH EXTERNAL ORIGIN. Based on the above-mentioned literature we classified seedlings and saplings according to their dispersal mode as either animal-, wind- or gravity-dispersed. As we were interested in the permeability of different matrices for animals we excluded wind- and gravity-dispersed species. We further classified seedlings and saplings as recruitment with local or external origin. We considered seedlings and saplings as external recruits if no conspecific adult trees were present within the plot. We additionally checked the canopy directly above seedling and sapling plots for conspecifics as tree crowns can be protruding. We are aware of the methodological constraints of this method. For instance, it can lead to an underestimation of seed dispersal as we did not distinguish between male and female dioecious trees. Alternatively, it can cause an overestimation of seed dispersal if recruitment stems from adult trees that have died or been logged. Nevertheless, the method has been shown to provide valuable results on the importance of seed dispersal in tropical forests (Martínez-Ramos & Soto-Castro 1993; Melo *et al.* 2010).

DATA ANALYSES. All analyses were performed with R version 2.12.0 (R Development Core Team 2010). We used analyses of covariance (ANCOVA) to test effects of fragment quality measures as well as of the four forest fragment types surrounded by variable matrix habitat (ForFra, GraFra, PlaFra, AgrFra) on species richness and abundance of trees, seedlings and saplings separately for ES and LS species. We included the number of individuals as a covariate in the ANCOVAs for species richness as richness might increase with abundance (Gotelli & Colwell 2001). Tree species richness as well as seedling and sapling abundance data were $\ln(x + 0.5)$ -transformed *prior* to analyses to reach homogeneity of variances and normality

of residuals. Canopy cover and vegetation complexity were included as covariates in all models; light intensity only into seedlings and saplings models. Effects of covariates were corrected for each other using type II SS. Independent variables were excluded from the models through stepwise deletion starting with the least significant term ($P > 0.1$). We checked for differences in canopy cover, light intensity and vegetation complexity of the forest fragments using analyses of variance (ANOVAs). Differences between fragment types were analysed using Tukey's Honestly Significant Difference (Tukey's HSD) multiple pairwise comparison *post hoc* test ($P < 0.1$).

We applied non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity implemented in R package *vegan* version 2.0-1 (Oksanen *et al.* 2011) based on abundance data to detect differences between species composition among different forest fragment types. NMDS displays dissimilarities in community composition nonlinearly onto ordination space, can cope with nonlinear species responses and is not constrained by predictors (Oksanen 2011). We pooled tree, seedling and sapling species as community compositions of the three stage classes were not independent. We excluded rare species that only occurred once (singletons) and that were merely present in one plot (uniques) leaving 88 species (54 ES, 34 LS). Forest fragment quality measures and variable matrix habitat were fitted *post hoc* to the ordination; their effects were tested *via* random permutations (1000 iterations).

We moreover tested the effect of matrix habitat on the relative proportion of external recruitment of seedling and sapling individuals using ANOVAs. We did not consider forest fragment quality in these analyses as we believed it to be of low relevance to possible seed influx into forest fragments. Only animal-dispersed species were used as reference for percentages of total recruitment present per plot. Proportions were arcsine square root-transformed *prior* to analyses to reach model assumptions. We combined ES and LS individuals as we were interested in overall external recruitment. In two AgrFra plots no animal-dispersed seedlings occurred leaving 22 plots for analyses.

Results

TREES. We identified 121 tree species (70 ES, 51 LS) and 1440 tree individuals (902 ES, 538 LS; Appendix 2). ES tree species richness was neither significantly affected by forest fragment quality nor by matrix habitat (Table 3.1). It ranged from 8.3 (+1.8/-1.5) in ForFra to 12.7

(+ 1.4/- 1.2) in PlaFra (for back-transformed means positive/negative SEs stated separately; Fig. 3.2a). ES species richness highly significantly increased with increasing abundance of ES trees (Table 3.1). LS tree species richness significantly increased with higher canopy cover and tended to increase with enhanced vegetation complexity (Table 3.1). LS tree species richness was significantly affected by matrix habitat (*post hoc* comparisons: all *vs.* PlaFra $P < 0.001$). It was highest in ForFra (8.6 + 1.8/- 1.5) and lowest in PlaFra (1.0 + 0.7/- 0.5; Fig. 3.2a).

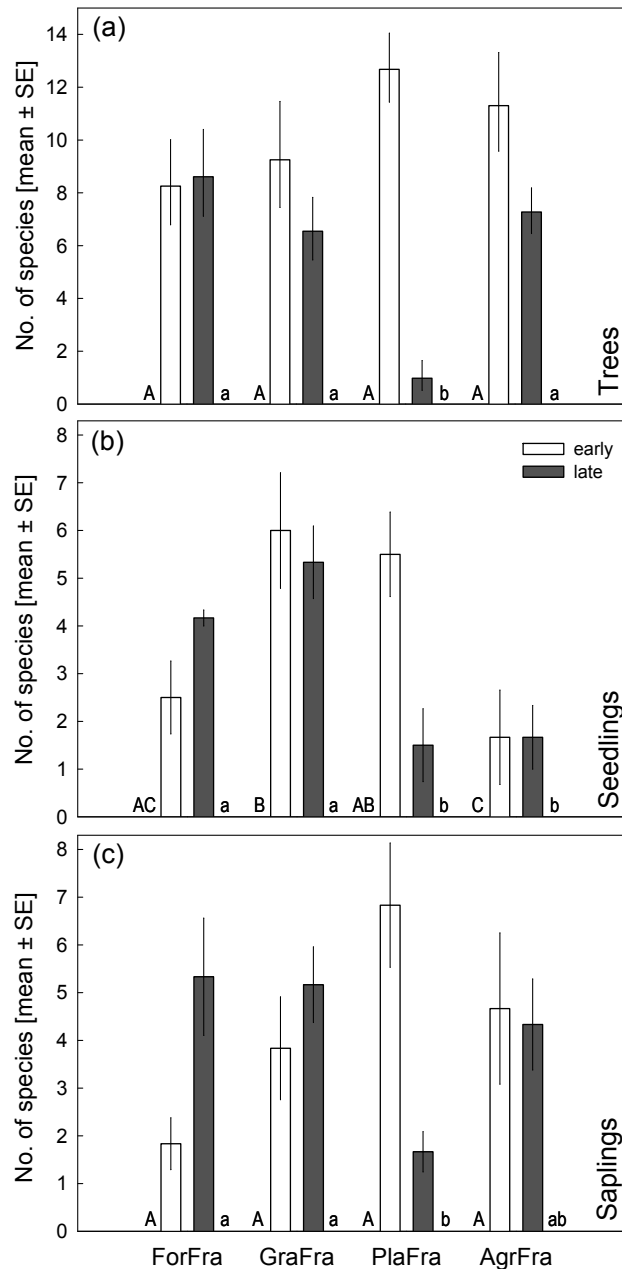


Figure 3.2. Species richness of early- (light bars) and late-successional (dark bars) trees, seedlings and saplings in forest fragments with variable matrix habitat. (a) Trees, (b) seedlings and (c) saplings in large natural forest fragments with forest matrix (ForFra) and in small forest fragments surrounded by natural grassland (GraFra), plantations (PlaFra) and agriculture (AgrFra). Shown are means \pm SE (back-transformed for trees), different letters (upper case = early-, lower case = late-successional species) indicate significant differences ($P < 0.1$) according to Tukey's HSD multiple pairwise comparison *post hoc* test.

Table 3.1. ANCOVA models testing the effect of forest fragment quality (canopy cover, light intensity, vegetation complexity) and matrix habitat on species richness and abundance of early- (ES) and late-successional (LS) trees, seedlings and saplings. Number of individuals is only included as a covariate into species richness models. Models either refer to untransformed (untrans) or ln-transformed (ln trans) data ($\ln(x + 0.5)$). Given are df-, R^2 , F - and P -values for full models after stepwise deletion of non-significant terms (ns) and all model parameters (values just before deletion); no. individuals = number of individuals, veg. complex. = vegetation complexity; ° $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	ES trees			LS trees			ES seedlings			LS seedlings			ES saplings			LS saplings		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
<i>Species richness</i>	ln-trans; $R^2 = 0.50$			ln-trans; $R^2 = 0.71$			untrans; $R^2 = 0.83$			untrans; $R^2 = 0.60$			untrans; $R^2 = 0.51$			untrans; $R^2 = 0.25$		
Full model	1,22	23.74	***	4,19	14.75	***	7,16	16.82	***	4,19	9.58	***	1,22	25.25	***	3,20	3.57	*
Canopy	1	0.73	ns	1	6.67	*	1	16.83	***	1	0.02	ns	1	2.12	ns	1	0.03	ns
No. individuals	1	23.74	***	1	0.68	ns	1	26.32	***	1	0.78	ns	1	25.25	***	1	0.12	ns
Light intensity	-	-	-	-	-	-	1	13.11	**	1	5.79	*	1	0.00	ns	1	0.81	ns
Veg. complex.	1	2.77	ns	1	3.57	°	1	5.03	*	1	1.80	ns	1	0.53	ns	1	1.63	ns
Matrix habitat	3	1.69	ns	3	3.32	*	3	9.47	***	3	10.43	***	3	0.77	ns	3	3.57	*
<i>Abundance</i>	untrans; $R^2 = 0.48$			untrans; $R^2 = 0.53$			ln-trans; $R^2 = 0.49$			ln-trans; $R^2 = 0.60$			ln-trans; $R^2 = 0.59$			ln-trans; $R^2 = 0.55$		
Full model	2,21	11.53	***	1,22	26.72	***	4,19	6.45	**	3,20	12.63	***	4,19	9.20	***	3,20	10.52	***
Canopy	1	15.33	***	1	26.72	***	1	0.13	ns	1	1.15	ns	1	1.52	ns	1	3.64	°
Veg. complex.	1	9.74	**	1	1.34	ns	1	6.58	*	1	1.69	ns	1	15.02	**	1	1.36	ns
Matrix habitat	3	0.90	ns	3	2.61	°	3	5.94	**	3	12.63	***	3	7.10	**	3	10.52	***

ES tree abundance decreased significantly with increasing canopy cover and increased significantly with higher vegetation complexity (Table 3.1). ES tree abundance was not significantly affected by matrix habitat (Table 3.1). It was similarly high in all fragment types (range: 29.3 ± 5.3 – 32.8 ± 7.0) but much higher in PlaFra (58.0 ± 6.2 ; Fig. 3.3a). LS tree abundance increased with higher canopy cover and was marginally significantly affected by matrix habitat (Table 3.1). LS tree abundance showed the opposite pattern of ES tree abundance with similar values in all fragment types (range: 18.5 ± 2.6 – 39.0 ± 7.0) but much lower abundance in PlaFra (3.5 ± 1.5 ; Fig. 3.3a).

SEEDLINGS. The total seedling community consisted of 61 species (33 ES, 28 LS) and 692 individuals (294 ES, 398 LS; Appendix 2). All measures of forest fragment quality significantly affected ES seedling species richness: it increased with decreasing canopy cover and with increasing light intensity and vegetation complexity (Table 3.1). ES seedling species richness varied significantly between fragment types with variable matrix habitat (*post hoc* comparisons: ForFra vs. GraFra $P = 0.085$, GraFra vs. AgrFra $P = 0.024$, PlaFra vs. AgrFra $P = 0.052$). ES seedling species richness was high in GraFra (6.0 ± 1.2) and PlaFra (5.5 ± 0.9) and low in ForFra (2.5 ± 0.8) and AgrFra (1.7 ± 1.0 ; Fig. 3.2b). It increased with increasing ES seedling abundance. LS seedling species richness increased significantly with increasing relative light intensity (Table 3.1). It showed significant differences between fragment types with natural and modified matrix habitat (*post hoc* comparisons: ForFra vs. PlaFra $P = 0.037$, ForFra vs. AgrFra $P = 0.053$, GraFra vs. PlaFra $P = 0.002$, GraFra vs. AgrFra $P = 0.003$). LS seedling species richness was highest in ForFra (4.2 ± 0.2) and GraFra (5.3 ± 0.8) and lowest in PlaFra (1.5 ± 0.8) and AgrFra (1.7 ± 0.7 ; Fig. 3.2b).

ES seedling abundance increased significantly with increasing vegetation complexity (Table 3.1). It differed significantly between fragment types (*post hoc* comparisons: ForFra vs. PlaFra $P = 0.067$, GraFra vs. AgrFra $P = 0.070$, PlaFra vs. AgrFra $P = 0.015$) and showed a similar picture as species richness with highest numbers of individuals in PlaFra ($16.2 + 11.8/- 6.9$) and GraFra ($9.5 + 4.2/- 3.0$) and lowest numbers in ForFra ($2.1 + 1.3/- 0.9$) and AgrFra ($1.1 + 1.4/- 0.8$; Fig. 3.3b). LS seedling abundance was not significantly affected by forest fragment quality (Table 3.1) It showed significant differences among fragment types with natural and modified matrix habitat (*post hoc* comparisons: ForFra vs. PlaFra $P = 0.002$, GraFra vs. AgrFra $P = 0.004$, GraFra vs. PlaFra $P < 0.001$, GraFra vs. AgrFra

Results

$P = 0.002$). LS seedling abundance was highest in ForFra (21.7 + 7.4/- 5.6) and GraFra (26.9 + 9.6/- 7.1) and lowest in PlaFra (1.2 + 1.1/- 0.7) and AgrFra (1.7 + 1.5/- 0.9; Fig. 3.3b).

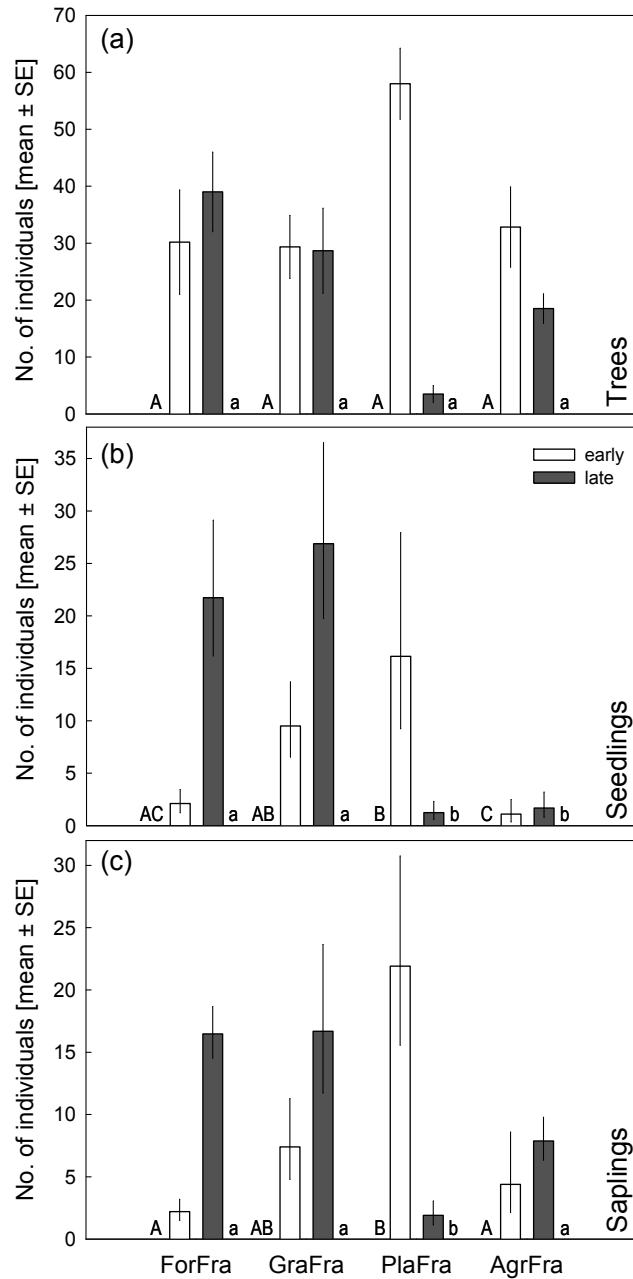


Figure 3.3. Abundance of early- (light bars) and late-successional (dark bars) trees, seedlings and saplings in forest fragments with variable matrix habitat. (a) Trees, (b) seedlings and (c) saplings in large natural forest fragments with forest matrix (ForFra) and in small forest fragments surrounded by natural grassland (GraFra), plantations (PlaFra) and agriculture (AgrFra). Shown are means \pm SE (back-transformed for trees), different letters (upper case = early-, lower case = late-successional species) indicate significant differences ($P < 0.1$) according to Tukey's HSD multiple pairwise comparison *post hoc* test.

SAPLINGS. The total sapling community comprised 81 species (47 ES, 34 LS) and 614 individuals (308 ES, 306 LS). ES sapling species richness was neither affected by forest fragment quality nor by matrix habitat (Table 3.1). ES sapling species richness ranged from 1.8 ± 0.5 in ForFra to 6.8 ± 1.3 in PlaFra (Fig. 3.2c) and increased significantly with higher ES sapling abundance (Table 3.1). LS sapling species richness was not significantly affected by forest fragment quality (Table 3.1). It differed significantly between fragment types (*post hoc* comparisons: ForFra *vs.* PlaFra $P = 0.042$, GraFra *vs.* PlaFra $P = 0.055$). LS sapling species richness showed a similar pattern as observed for trees and varied little between all fragment types (range: $4.3 \pm 1.0 - 5.3 \pm 1.2$) but PlaFra, where richness was much lower (1.7 ± 0.4 ; Fig. 3.2c).

ES sapling abundance increased significantly with higher vegetation complexity (Table 3.1). It showed similar results as ES sapling richness and was significantly affected by matrix habitat (*post hoc* comparisons: ForFra *vs.* PlaFra $P = 0.012$, PlaFra *vs.* AgrFra $P = 0.093$). Abundances ranged from $2.2 (+ 1.0/- 0.7)$ to $7.4 (+ 3.9/- 2.6)$ in all fragment types but PlaFra where abundance was much higher ($21.9 + 8.8/- 6.3$; Fig. 3.3c). LS sapling abundance tended to increase with higher canopy cover (Table 3.1). It varied significantly between fragment types (*post hoc* comparisons: ForFra *vs.* PlaFra $P < 0.001$, GraFra *vs.* PlaFra $P < 0.001$, PlaFra *vs.* AgrFra $P = 0.027$). Abundance was highest in ForFra ($16.5 + 2.2/- 2.0$) and GraFra ($16.7 + 7.0/- 5.0$), intermediate in AgrFra ($7.9 + 1.9/- 1.5$) and lowest in PlaFra ($1.9 + 1.2/- 0.8$; Fig. 3.3c).

FOREST FRAGMENT QUALITY. Canopy cover varied significantly between fragment types with variable matrix habitat ($F_{3,20} = 8.0$, $P = 0.001$; *post hoc* comparisons all *vs.* PlaFra: ForFra $P < 0.001$, GraFra $P = 0.021$, AgrFra $P = 0.008$). Canopy cover was highest in ForFra ($89.8\% \pm 2.4$), intermediate in GraFra ($83.8\% \pm 2.4$) and AgrFra ($85.7\% \pm 2.1$) and lowest in PlaFra ($70.2\% \pm 4.5$). Light intensity did not differ significantly between fragment types ($F_{3,20} = 1.35$, $P = 0.29$). It was lowest in AgrFra ($0.22\% \pm 0.04$), intermediate in ForFra and GraFra ($1.01\% \pm 0.45$; $1.27\% \pm 0.68$) and highest in PlaFra ($1.66\% \pm 0.64$). Vegetation complexity did not vary significantly between fragment types with variable matrix habitat ($F_{3,20} = 0.09$, $P = 0.96$). It gradually increased from 1.91 ± 0.06 in PlaFra to 1.97 ± 0.06 in ForFra.

COMMUNITY COMPOSITION. NMDS significantly separated the community composition of cumulative tree, seedling and sapling species by fragment types with variable matrix habitat

(two convergent solutions, two dimensions, stress = 0.15, $R^2 = 0.72$, $P < 0.001$; Fig. 3.4). ForFra and GraFra communities were located close together with overlapping 95% confidence interval ellipses of their class centroids. PlaFra and AgrFra formed completely disconnected groups without overlapping of class centroid ellipses. Forest fragment types with natural matrices were arranged along a gradient of increasing canopy cover towards ForFra ($R^2 = 0.55$, $P < 0.001$). PlaFra was located in the opposite direction of this gradient. ES and LS species were equally distributed in ForFra, GraFra and AgrFra, but in PlaFra no LS species occurred. Light intensity and vegetation complexity had no significant influence on community composition ($R^2 = 0.01$, $P = 0.86$; $R^2 = 0.03$, $P = 0.75$).

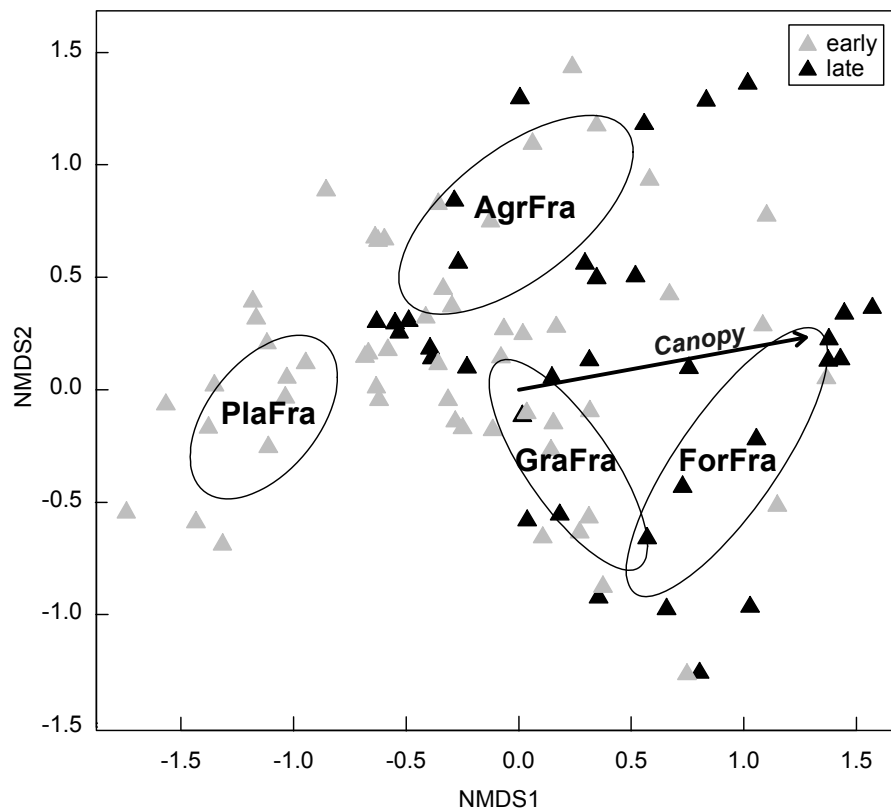


Figure 3.4. NMDS biplot of cumulative tree, seedling and sapling species scores ($n = 88$) showing community composition separated by successional status as early- (light triangles) and late-successional (dark triangles) species in large natural forest fragments with forest matrix (ForFra) and in small forest fragments surrounded by natural grassland (GraFra), plantations (PlaFra) and agriculture (AgrFra). Fitted fragment types are shown with 95% confidence interval ellipses of their class centroids, the arrow points along the gradient of increasing canopy cover.

RECRUITMENT WITH EXTERNAL ORIGIN. Animal-dispersed species included 88% of total species richness of all stage classes found (Appendix 2). Relative external recruitment of seedling individuals did not vary significantly between fragment types with variable matrix

habitat ($F_{3,18} = 0.27$, $P = 0.85$). It ranged from 20.6% (+ 10.2/- 8.6) in ForFra to 28.4% (+ 9.7/- 8.8) in PlaFra. Relative external recruitment of sapling individuals was not significantly affected by matrix habitat ($F_{3,20} = 0.58$, $P = 0.68$). It showed similar values for all fragment types and ranged from 22.2% in PlaFra (+ 6.3/- 5.7) to 37.0% (+ 13.6/- 12.6) in AgrFra.

Discussion

Tree species richness and abundance were rather impacted by forest fragment quality than by matrix habitat. LS tree species were strongly diminished in PlaFra, where canopy cover was significantly lower. Effects of forest fragment quality and matrix habitat were more pronounced in the young stages. Species richness and abundance of tree recruits showed a general decline in fragments with modified matrices regardless of their successional status, which was corroborated in the NMDS. Matrices did seemingly not act as an impenetrable barrier to seed dispersal as seed influx occurred in all fragment types.

TREES. Tree species richness and abundance were affected by high canopy cover decreasing ES and increasing LS trees. Tree communities did not respond to variable matrix habitat in all fragment types but PlaFra where ES species richness and abundance were strongly elevated while LS species were diminished. Findings are similar to those of others who also barely found effects of forest fragmentation on the adult tree community (Lawes *et al.* 2007; Farwig *et al.* 2008b). One possible explanation might be that trees are long-lived and effects of human impact, rapidly increasing only in the last decades, might not be visible yet.

In PlaFra the prevalence of ES at the expense of LS species was in line with our expectations and has been reported by others who also found a decline in LS trees in fragmented forests (Laurance *et al.* 1998; Laurance *et al.* 2006; Kirika *et al.* 2010). This pattern was seemingly caused by changes of forest fragment quality in terms of abiotic conditions. Canopy cover was significantly reduced and light availability was highest in PlaFra compared to all other fragment types, which thus seemingly supplied the most beneficial conditions for ES species. Moreover, PlaFra might still be in the process of succession. Since the time of plantation establishment (before 1972) buffer zones have only gradually been increased in size between 1972 and 1998 (Edwards & Roberts 2006). Yet, if local sources of propagules and seed dispersers are present and plantation management in the understory is

moderate, plantations are able to aid forest succession (Brockerhoff *et al.* 2008 and references therein). However, the lack of LS adult trees in PlaFra remains alarming as it might impede further succession.

RECRUITMENT. Recruitment was generally higher in forest fragments with natural matrices compared to fragments with modified matrices. Moreover, fragments with natural matrix habitat had a much higher richness and abundance of LS species than fragments with modified surroundings. This is in line with results of others reporting a general decline of seedlings and particularly LS species in forest fragments (Cordeiro & Howe 2001; Benítez-Malvido & Martínez-Ramos 2003a; Farwig *et al.* 2008b; Kirika *et al.* 2010).

Decreasing species richness and abundance of recruits can be a consequence of alterations of abiotic or of biotic conditions in modified forests (Ramírez-Marcial 2003). For example, light availability is regarded the most important regulator of seedlings performance (Pacala *et al.* 1996). Yet, in our study light intensity on the forest floor did not significantly differ between fragment types. Nevertheless, it was by trend lowest in AgrFra. This was presumably caused by interspecific competition of a dominant, large, semi-woody herb (*Isoglossa woodi*) shading out the forest floor (Griffiths *et al.* 2007). In PlaFra on the other hand canopy cover was significantly reduced reflecting the lack of LS tree density there, which might also be responsible for their lacking recruitment.

Furthermore, changes in biotic interactions appear possible. For instance, Farwig *et al.* (2008b) argued that the reduction in relative seedling species richness due to fragmentation might have been caused by diminished frugivore abundance as no differences in light intensity occurred between main forest and fragments. However, we consider this unlikely in our case: in previous studies in the same scarp forest fragments we could demonstrate that frugivore abundance and fruit removal were not negatively affected in forest fragments with modified matrices (Neuschulz *et al.* 2011). Moreover, antagonistic processes, such as seed predation and seedling herbivory may increase in fragmented forests with negative impact on recruitment (Donoso *et al.* 2003; Benítez-Malvido & Lemus-Albor 2005). In line with these findings, we could also prove elevated seed predator densities as well as increased seed predation in scarp forest fragments with modified matrix habitat in further studies (see chapter 2). Presumably, modified matrices, especially sugarcane, acted as a barrier for large

predators leading to an ecological release of seed predators (Terborgh *et al.* 2008), which in turn diminished recruitment (Asquith *et al.* 1997).

In consequence, altered forest fragment quality in combination with modified matrices seems to affect abiotic as well as biotic conditions in forest fragments. Thereby, general seedling and sapling recruitment is hampered, particularly recruitment of LS species. This suggests that tree regeneration might be at stake in the long term.

COMMUNITY COMPOSITION. Cumulative community composition of all three stage classes was affected by forest fragment quality and by matrix habitat. Fragment types with natural matrix habitat were very similar in composition, whereas fragment types with modified matrices formed separate groups indicating compositional shifts. This shift comprised the increase of ES at the expense of LS species.

These changes in community composition can presumably be related to differences in canopy cover between fragment types with natural and modified matrix habitat. This was corroborated by the significant gradient of increasing canopy cover pointing towards fragment types with natural matrices and away from those with modified matrix habitat. As canopy openings have been demonstrated to be quickly colonized by ES species (Kariuki & Kooyman 2005) this might also explain their predominance in fragment types with modified matrix habitat. The proliferation of ES species can have severe consequences for nutrient cycling, carbon storage and forest regeneration dynamics. For instance, less carbon is stored in ES species and nutrient cycles are accelerated due to their shorter life time compared to LS species (Laurance *et al.* 2006; Laurance *et al.* 2011). As a result, this calls for the necessity of large natural forests in order to provide connectivity and serve as source of propagules to maintain community composition and equal proportions of ES and LS species.

RECRUITMENT WITH EXTERNAL ORIGIN. Modified matrices did presumably not act as sharp barriers for seed dispersers. Recruitment originating from animal-mediated seed influx was similarly high in all fragment types. This contrasts with our expectation of higher external recruitment in fragments with natural matrix habitat.

Our definition of external recruitment is rather conservative: recruits classified as local might have originated from adult trees within the plot but also from adults elsewhere (Melo *et al.* 2010). We thus might have underestimated external recruitment in fragments

with natural matrix habitat because of the higher density of many adult tree species compared to fragments with modified matrices.

Nevertheless, our findings are in line with Herrera *et al.* (2011) who also did not find negative effects of the matrix on seed dispersal into fragments. In addition, we could show that bird frugivores were present in all fragment types in the same study region (Neuschulz *et al.* 2011) indicating frequent movements of birds among patches (García & Chacoff 2007). In consequence, plant-frugivore interactions, such as seed dispersal can be maintained to a certain degree even if matrix and remaining habitat patches greatly differ (Bender & Fahrig 2005). Some matrix components, such as isolated trees serving as focal points, corridors or the matrix quality itself may contribute to buffering negative matrix effects by facilitating seed disperser movement and thereby enhance landscape connectivity (García & Bañuelos 2003; Herrera & García 2009). This underlines the important role of structurally diverse landscapes including forest fragments as stepping-stones for seed dispersers.

Conclusions

Our study demonstrates that forest fragment quality and matrix habitat only slightly impacted trees as merely in PlaFra ES predominated at the expense of LS species. Yet, seedling and sapling establishment of particularly LS species were hampered in fragments with modified matrices in comparison to fragments with natural matrix habitat, which was supported by the clear separation of these groups in the NMDS. This shift in community composition might have been caused by reduced canopy cover and increased light intensity in fragments with modified matrix habitat. External recruitment was present in all fragments indicating permeability of the structurally diverse landscape for seed dispersers. To conclude, alterations of forest fragment quality and modified matrix habitat showed negative consequences for the young stages during regeneration highlighting their important role as indicators of human impact. The structurally complex landscape comprising fragments with both natural and modified matrix habitat seems to buffer negative effects of forest fragmentation. Such landscapes contribute to connectivity by providing stepping stones for seed dispersers, yet cannot replace natural forests. These natural forest fragments are essential sources of propagules to ensure forest regeneration through, *e.g.* seed influx into

modified habitats. Thus, conservation management needs to consider connectivity across remaining natural habitat patches.

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4 Forest fragment quality rather than matrix habitat shapes herbivory on tree recruits

With Lena Fischer and Nina Farwig

Abstract. Deforestation and fragmentation alter antagonistic interactions, such as herbivory on tree recruits with possible consequences for regeneration. Here, we assessed the impact of forest fragment quality in terms of structural characteristics and matrix habitat on arthropods and leaf damage on tree seedlings and saplings in KwaZulu-Natal, South Africa. We quantified forest fragment quality regarding tree diversity, vertical vegetation complexity and canopy cover. We compared arthropod predator and herbivore abundances, insect herbivory and pathogen infestation among scarp forest fragments with variable matrix habitat: two fragment types with natural heterogeneous matrices, *i.e.* large fragments with forest matrix and small fragments surrounded by grassland as well as two small fragment types with modified homogeneous matrices, *i.e.* eucalypt plantations and sugarcane agriculture. Forest fragment quality increased arthropod predator and decreased arthropod herbivore abundance. Herbivory responses to fragment quality were diverging with tree diversity decreasing seedling, but increasing sapling herbivory while canopy cover increased herbivory of tree recruits generally. Fragment quality had no effect on pathogen infestation. In general, matrix habitat showed no pronounced effects on arthropods and leaf damage. Merely, seedling pathogen infestation and sapling herbivory tended to vary with matrix habitat. Trophic interactions between arthropod predators, herbivores and herbivory seemed to be weak and diffuse in scarp forest fragments. We assume differences in herbivore species compositions and plant palatability to be responsible for contrasting effects on arthropods and herbivory. Overall, herbivory on tree recruits seemed to be mediated by forest fragment quality rather than by matrix habitat, but interactions between arthropod predators and herbivores appeared to be highly complex.

Key words. Diversity-herbivory relationships, habitat quality, KwaZulu-Natal, leaf damage, pathogen infestation, plant-animal-interactions, saplings, scarp forest, seedlings.

Introduction

Worldwide human activities, such as deforestation, habitat fragmentation and agricultural intensification pose a threat to biodiversity (Sala *et al.* 2000; Tylianakis *et al.* 2008). This is particularly severe in forests, which provide habitat for more than half of the known terrestrial plant and animal species (MEA 2005). The consequences of this biodiversity decline for ecological processes are far from being understood (Balvanera *et al.* 2006). Accordingly, antagonistic interactions, such as insect herbivory and leaf fungal pathogen infestation might be subject to changes with potentially critical outcomes for forest regeneration.

Herbivory by insects is the predominant form of leaf damage in (sub-) tropical forests, often accompanied by pathogen infestation and far exceeding mammalian herbivory (García-Guzmán & Dirzo 2001; Ruiz-Guerra *et al.* 2010). Herbivores and pathogens play an important role in plant species coexistence as they either directly influence plants through consumption/infestation or indirectly affect their competitiveness, which can have consequences for plant diversity (Hulme 1996). Consequently, such forms of leaf damage on tree seedlings and saplings do not only affect the survival, growth and productivity of individual plants, but also have the potential to alter dynamics and structure of (sub-) tropical forests (Burdon 1993; Hoshizaki *et al.* 1997; Maron & Crone 2006).

Insect herbivory and leaf fungal pathogen infestation of woody seedlings and saplings have shown to be affected by forest fragmentation (Krüss & Tschardtke 1994; Santos & Benítez-Malvido 2012). This could be ascribed to modifications of structural characteristics in forest fragments (*e.g.* Saunders *et al.* 1991; Montgomery & Chazdon 2001; Harvey *et al.* 2006). For instance, a decline of tree diversity in forest fragments has been found to increase herbivory and pathogen infestation and *vice versa* (Jactel *et al.* 2006; Jactel & Brockerhoff 2007; Kaitaniemi *et al.* 2007; Haas *et al.* 2011). The reduced susceptibility of diverse plant communities to insect herbivory has been explained by the concept of 'associational resistance' comprising two hypotheses: (1) specialist herbivores are assumed to find fewer resources in more diverse plant communities as non-host plant abundance increases ('resource concentration hypothesis', Tahvanai & Root 1972; Root 1973); (2) higher diversity is believed to involve an increase in structural and resource diversity, such as alternative

prey, shelter and additional food for natural enemies like arthropod predators and parasitoids. This should entail a reduction of herbivores and thereby also decrease herbivory ('enemies hypothesis', Root 1973). In line with the second hypothesis, some authors found an increase of insect herbivory in small fragments caused by lower enemy abundance (*e.g.* Terborgh *et al.* 2001). The decline of pathogen transmission in diverse systems has been explained by increased competition and problems in host-finding (Mitchell *et al.* 2002; Roscher *et al.* 2007), similar to the 'resource concentration hypothesis'. In contrast, some studies also found an amplification of insect herbivory and pathogen infestation with increases in tree species richness (Vehviläinen *et al.* 2007; Scherber *et al.* 2010). Such positive diversity-herbivory and diversity-disease relationships have been attributed to spillover effects of generalist herbivores ('associational susceptibility', White & Whitham 2000) or by a wide host range for pathogens (Keesing *et al.* 2010). Fragmentation effects on pathogen infestation have rarely been investigated (but see Benítez-Malvido *et al.* 1999; Holdenrieder *et al.* 2004). Yet, as many fungal pathogens depend on insect wounds to infect plants (García-Guzmán & Dirzo 2001), similar responses of pathogens and insect herbivores are expected in relation to fragmentation (Benítez-Malvido *et al.* 1999).

Numerous studies have recently stressed that considering not only forest fragments and their quality, but also the matrix surrounding these fragments, may be equally important for conservation (Kupfer *et al.* 2006; Vandermeer & Perfecto 2007; Perfecto & Vandermeer 2010). Depending on structure and permeability, matrices can on the one hand complement natural habitat, facilitate dispersal among habitat remnants or buffer negative effects of forest fragmentation. On the other hand they might as well function as ecological traps for native species (Kupfer *et al.* 2006; Brockerhoff *et al.* 2008 and references therein). Thus, low-contrast matrices composed of diverse, structurally complex landscapes that resemble the natural habitat might facilitate the movement of insectivorous vertebrates (Tschamntke *et al.* 2005). Several studies have shown that insectivorous vertebrates significantly reduce the abundance of herbivores and thereby enhance plant performance (*e.g.* Greenberg *et al.* 2000; Kalka *et al.* 2008). In addition, the matrix may offer additional or complementary resources for both predators and herbivores or even link together different required habitat elements for many species in order to complete their life cycles (Haynes *et al.* 2007; Diekötter *et al.* 2007). Contrarily, high-contrast matrices comprising homogenous, structurally poor elements might hamper the movement of arthropod predators or

insectivorous vertebrate predators leading to a release of herbivores and thereby increase herbivory (*e.g.* Kalka *et al.* 2008). In sum, matrix habitat may play an essential role in shaping leaf damage on tree recruits. Studies on insect herbivory and leaf fungal pathogen infestation have investigated fragmentation and edge effects (*e.g.* Benítez-Malvido & Lemus-Albor 2005; Faveri *et al.* 2008; Ruiz-Guerra *et al.* 2010). Yet, to our knowledge, no study on leaf damage of the naturally grown woody seedling and sapling community in subtropical forest fragments has jointly assessed the effects of fragment quality and matrix habitat.

In this study we examined the impact of forest fragment quality and matrix habitat on the arthropod predator (hereafter predators, other predators are specified) and insect herbivore (herbivore) community and on leaf damage of woody seedlings and saplings in scarp forest fragments in KwaZulu-Natal, South Africa. We assessed the influence of forest fragment quality in terms of tree diversity, vertical vegetation complexity and canopy cover on arthropods, herbivory and pathogens. We further compared arthropod abundance, insect herbivory and leaf pathogen infestation among forest fragments with variable matrix habitat: two fragment types with natural heterogeneous matrices, *i.e.* large fragments with forest matrix and small fragments surrounded by grassland as well as two fragment types with modified homogeneous matrices, *i.e.* eucalypt plantations and sugarcane agriculture. We expected (1) forest fragment quality to enhance predator abundance and thereby reduce herbivore abundance and herbivory. Further, we hypothesized (2) that natural matrix habitat increases predator abundance due to higher structural diversity and thereby controls herbivores and herbivory in fragment surrounded by natural matrices. We accordingly anticipated (3) that modified matrix habitat hampers predator movement and leads to increased herbivore abundance and consequently herbivory as well as concurrent leaf fungal pathogen infestation in fragments with modified matrices.

Methods

STUDY AREA AND DESIGN. 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'E) and Oribi Gorge (OG; 30°41'S–30°45'S, 30°10'E–30°18.5'E) nature reserves. Scarp forest forms a transition zone between Afromontane forest and Indian Ocean coastal belt forest. It is located on south- and southeast-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 (Lawes 1990; Eeley *et al.* 1999). They belong to the summer rainfall (October–March) subtropical climate zone and feature seasonal differences with an annual temperature range from 4 to 32°C and a rainfall range from 440 to 1400 mm (von Maltitz *et al.* 2003).

We studied scarp forest fragments surrounded by four different matrix habitat types, *i.e.* two natural heterogenous matrices within the two nature reserves and two modified homogenous matrix habitat types located outside the nature reserves. Forest fragments in natural matrix habitat were: (1) large natural forest fragments with forest matrix (ForFra) within two forest blocks (total size: VC 130 ha, OG 822 ha [henceforth we always report means \pm 1 SE], canopy cover: $89.8 \pm 2.2\%$, altitudinal range: 220–390 m asl) and (2) small forest fragments surrounded by natural grassland containing isolated trees and bushes (GraFra), kept open due to microclimatic conditions, grazing pressure and fire events (size: 2.3 ± 0.9 ha, canopy cover: $83.8 \pm 2.2\%$, altitudinal range: 340–480 m asl). Small fragments in modified matrix habitat comprised: (1) forest fragments surrounded by plantations (PlaFra) consisting of small remnant stretches of native forest as buffer zones of nearby streams within eucalypt plantations (major timber of the region, size: 0.6 ± 0.3 ha, canopy cover: $70.2 \pm 4.1\%$, altitudinal range: 480–510 m asl) and (2) forest fragments surrounded by agriculture (AgrFra), *i.e.* large sugarcane fields (predominant crop of the region, size: 3.2 ± 0.7 ha, canopy cover: $85.7 \pm 1.9\%$, altitudinal range: 390–580 m asl).

We established a total of 24 study plots, *i.e.* six replicates per forest fragment type surrounded by variable matrix habitat. Minimal distance between plots was 500 m except for PlaFra, which were at least 200 m apart. The replicates of fragment types per different matrix habitat were spatially clustered. However, both regions experience highly comparable abiotic conditions, *e.g.* topography, soil (sandstone) and climate (orographic rainfall, strong winds; von Maltitz *et al.* 2003). Moreover, they feature a similar tree species composition (see Appendix 2) and are exposed to comparable land-use modifications (sugarcane fields, timber plantations).

ARTHROPOD COMMUNITY. Plots were established as a cross of two 30 \times 10-m transects (500 m²). This cross was divided into 20 5 \times 5-m subplots (25 m²). We collected one beating

sample in every second of these subplots ($n = 10$) to assess the arthropod fauna in each study plot. We used a wooden club and a fabric funnel connected to a collecting bottle filled with 70% ethyl alcohol. Each beating sample consisted of ten standardized beats on randomly selected seedlings and saplings within the subplots. Arthropods were separated from plant material and debris, preserved in 70% ethyl alcohol, identified to order level and grouped into the feeding guilds predators (including parasitoids) and herbivores (Scholtz & Holm 1985; Picker *et al.* 2004). All other arthropods not belonging to these two categories were used to calculate relative abundances of predators and herbivores (hereafter arthropod or predator/herbivore abundance). Slugs and snails were not included in the assessment.

LEAF DAMAGE ON SEEDLINGS AND SAPLINGS. In the same alternating ten 5×5 -m subplots described above we established ten 1-m^2 seedling plots (10 m^2) as well as ten 5-m^2 sapling plots (50 m^2) that included the seedling plots. We assessed leaf damage on all seedlings with a diameter of < 1 cm at their base or < 75 cm high and all saplings with a diameter of < 5 cm at their base or > 75 cm high. Furthermore, we recorded the number of leaves of seedlings and saplings. Leaves of all seedlings and saplings were examined for two categories of leaf damage: insect herbivory and pathogen infestation. We defined herbivory as the removal of photosynthetic tissue (Schuldt *et al.* 2010) including damage caused by leaf chewing, galling, mining and leaf sucking. We classified leaf areas showing blight, chlorotic or necrotic spots and mouldy covering as leaf fungal pathogen infestation (Benítez-Malvido & Lemus-Albor 2005). Visual estimation of the percentages of both damage categories was conducted by one person only (L. Fischer) to avoid estimation bias. Damage rates were calculated per seedling and sapling individual by summing up the percentages for each leaf. The sum was divided by the number of inspected leaves per plant individual. We randomly sampled 30 leaves per plant. We randomly selected additional seedlings and saplings within the 5×5 -m subplots to achieve a minimum sampling effort of ten seedlings and saplings, respectively.

FOREST FRAGMENT QUALITY. To be able to evaluate forest fragment quality we assessed three environmental parameters, *i.e.* tree diversity, vertical vegetation complexity (henceforth vegetation complexity) and canopy cover. We assessed tree diversity by mapping all adult trees with a diameter at breast height of > 5 cm or > 400 cm high on the whole cross transect described above (500 m^2). Species were identified using Boon (2010), van Wyk and van Wyk

(2007) and Coates Palgrave (2005); species nomenclature follows Coates Palgrave (2005; see Appendix 2). Diversity of trees was calculated using Shannon index H . In the same alternating ten 5×5 -m subplots described above we assessed vegetation complexity. 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 H , to calculate vegetation complexity as suggested by Bibby *et al.* (2000) at each of the ten subplots and then averaged values for each plot. We estimated the percentage of canopy cover at two points directly adjacent to the ten sapling plots ($n = 20$) using a sighting tube (4×10 cm) and averaged estimations across plots.

DATA ANALYSES. All analyses were performed with R 2.14.1 (R Development Core Team 2011). We tested the three forest fragment quality measures (tree diversity, vegetation complexity, canopy cover) for bicollinearity using Spearman's rank correlation. Tree diversity and vegetation complexity were slightly correlated (Spearman's $\rho = 0.41$, $P = 0.045$), whereas tree diversity and canopy cover ($\rho = -0.16$, $P = 0.46$) as well as vegetation complexity and canopy cover ($\rho = -0.15$, $P = 0.48$) did not correlate. We used analyses of covariance (ANCOVA) to examine effects of fragment quality measures as well as of the four forest fragment types surrounded by variable matrix habitat (ForFra, GraFra, PlaFra, AgrFra) on abundance of arthropod predators and herbivores. Further, we tested effects of fragment quality, matrix habitat, and number of seedling/sapling leaves as a proxy for recruit age on percentages of herbivory and pathogen infestation of seedlings and saplings. We included arthropod predator and herbivore abundances into herbivory models. We checked model residuals for normality to reach model assumptions. Effects of covariates were corrected for each other using type II SS. Independent variables were excluded from the models through stepwise deletion starting with the least significant term ($P > 0.1$) and thus attaining minimum adequate models. Differences between forest fragments with variable matrix habitat were analysed using Tukey's Honestly Significant Difference (Tukey's HSD) multiple pairwise comparison *post hoc* test ($P < 0.1$). We furthermore used Spearman's rank correlations to test relationships between predator and herbivore abundances, seedling and sapling herbivory, seedling and sapling pathogen infestation as well as herbivory and pathogen infestation of seedlings and saplings.

Results

ARTHROPOD COMMUNITY. We recorded a total of 3,385 arthropods mainly consisting of insects, spiders, crustaceans and myriapods. Predators, the most abundant feeding guild, were primarily represented by spiders; herbivores by Coleoptera and Hemiptera. Other arthropods, not included in these two guilds, were predominantly decomposers, such as Collembola, crustaceans and myriapods.

Table 4.1. ANCOVA models testing the effects of forest fragment quality (tree diversity, canopy cover, vegetation complexity) and matrix habitat on relative arthropod abundances (predators, herbivores) and on herbivory and pathogen infestation of seedlings and saplings, respectively. Given are df-, R^2 -, F - and P -values for full models after stepwise deletion of non-significant terms (ns); path. = pathogen; veg. complex. = vegetation complexity; – not applicable; ° $P < 0.1$, * $P < 0.05$, ** $P < 0.01$.

	Relative arthropod abundance						Herbivory						Pathogen infestation					
	Predators			Herbivores			Seedlings			Saplings			Seedlings			Saplings		
Model fit	$R^2 = 0.18$			$R^2 = 0.19$			$R^2 = 0.37$			$R^2 = 0.21$			$R^2 = 0.17$			$R^2 = -$		
Parameter	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Full model	1,22	6.17	*	1,22	6.28	*	2,21	7.85	**	5,18	2.25	°	4,19	2.20	ns	–	–	–
Tree diversity	1	1.69	ns	1	1.50	ns	1	4.83	*	1	5.01	*	1	0.36	ns	1	2.69	ns
Vegetation complexity	1	6.17	*	1	2.95	ns	1	0.12	ns	1	0.02	ns	1	0.67	ns	1	0.04	ns
Canopy cover	1	0.01	ns	1	6.28	*	1	9.92	**	1	6.39	*	1	0.18	ns	1	0.09	ns
Leaves	–	–	–	–	–	–	1	1.10	ns	1	0.44	ns	1	3.16	°	1	0.21	ns
Matrix habitat	3	1.63	ns	3	0.46	ns	3	0.79	ns	3	3.06	°	3	2.48	°	3	1.03	ns

Abundance of predators was not significantly affected by tree diversity and canopy cover, but increased significantly with increasing vegetation complexity (Fig. 4.1a–c; Table 4.1). Predator abundance was not affected by matrix habitat (Fig. 4.2a; Table 4.1). Abundance of predators ranged from $34.3 \pm 4.0\%$ (PlaFra) to $60.7 \pm 4.6\%$ (GraFra; Fig. 4.2a). Herbivore abundance was not affected by tree diversity and vegetation complexity but decreased with increasing canopy cover. (Fig. 4.1d–f; Table 4.1). Matrix habitat showed no effect (Fig. 4.2a; Table 4.1). Abundance of herbivores ranged from $23.2 \pm 4.8\%$ (GraFra) to $34.3 \pm 4.9\%$ (AgrFra; Fig. 4.2a). Predator and herbivore abundances were not correlated (Spearman's $\rho = -0.18$, $P = 0.39$).

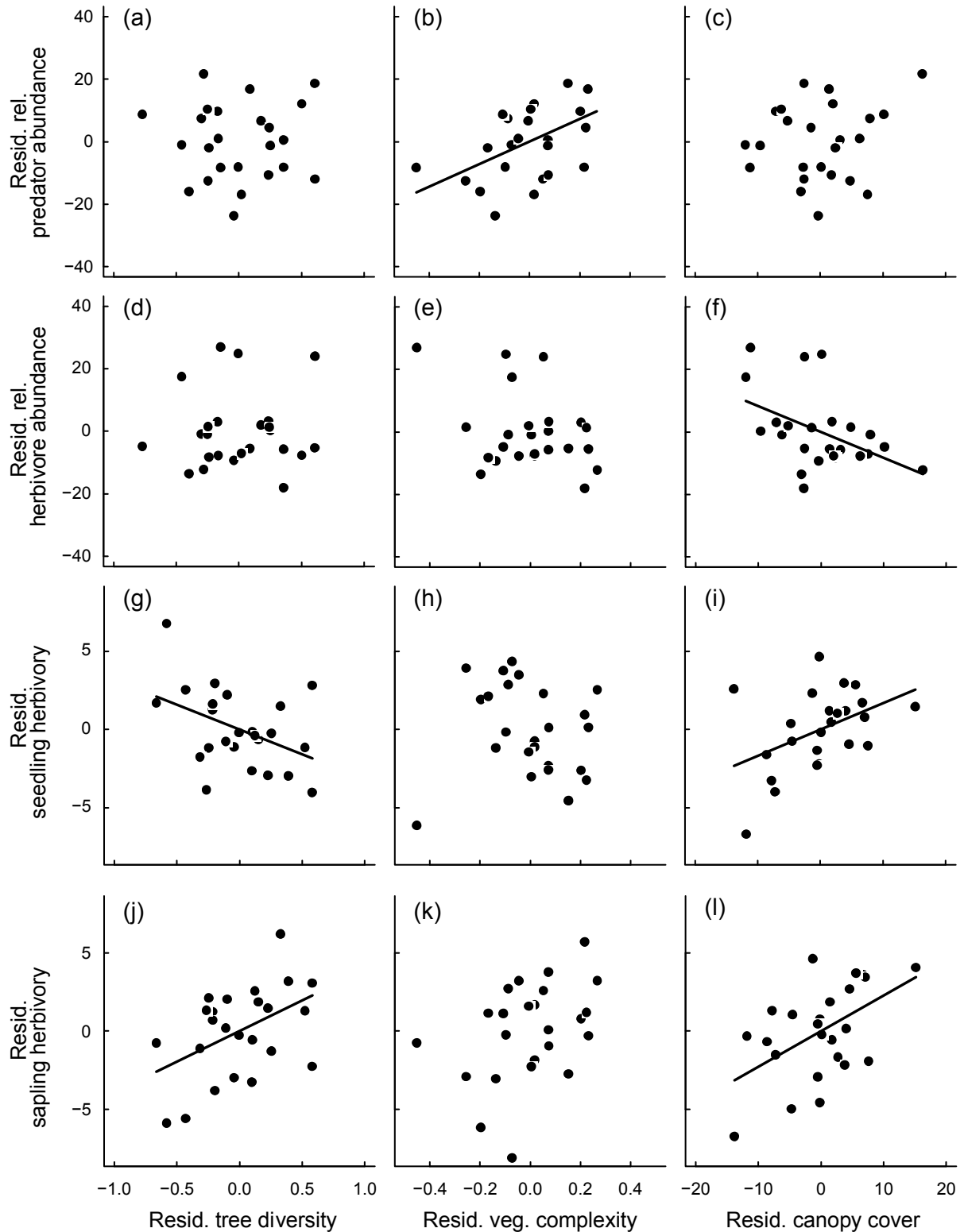


Figure 4.1. Arthropods and herbivory in response to forest fragment quality. Residual relative predator (a–c) and herbivore abundance (d–f) and residual herbivory of seedlings (g–i) and saplings (j–l) in relation to residual tree diversity, vegetation complexity and canopy cover. Resid. = residual, rel. = relative, veg. = vegetation.

INSECT HERBIVORY ON TREE RECRUITS. We examined a total of 9,009 leaves of 897 seedling individuals belonging to 71 species and 22,686 leaves of 876 sapling individuals of 91 sapling species. We further identified 1,440 individuals of 121 tree species (Appendix 2).

Average seedling herbivory was 10.8% (range: 0–70%). Seedling herbivory decreased significantly with increasing tree diversity, increased significantly with higher canopy cover and was not affected by vegetation complexity (Fig. 4.1g–i; Table 4.1). Matrix habitat had no effect (Fig. 4.2b; Table 4.1). Seedling herbivory ranged from $9.2 \pm 1.2\%$ (ForFra) to $10.4 \pm 1.2\%$ (AgrFra; Fig. 2b).

Average sapling herbivory was 12.5% (range: 0–80%). Sapling herbivory increased significantly with increasing tree diversity and canopy cover, while vegetation complexity had no effect (Fig. 4.1j–l; Table 4.1). Sapling herbivory tended to vary with matrix habitat (Fig. 4.2b; Table 4.1), but no specific differences were revealed by Tukey's HSD *post hoc* test. Herbivory on saplings ranged from $10.4 \pm 1.3\%$ (AgrFra) to $17.4 \pm 1.6\%$ (PlaFra; Fig. 4.2b). Seedling and sapling herbivory were not correlated (Spearman's $\rho = -0.014$, $P = 0.95$).

PATHOGEN INFESTATION OF TREE RECRUITS. Average pathogen infestation of seedlings was 5.7% (range: 0–80%). Pathogen infestation of seedlings was not affected by fragment quality (Table 1). Seedling pathogen infestation increased significantly with number of leaves (Table 1). Matrix habitat marginally significantly affected seedling pathogen infestation (Fig. 2c), but *post hoc* comparisons revealed no specific differences between forest fragments surrounded by variable matrix habitat. Seedling pathogen infestation ranged from $3.2 \pm 0.8\%$ (PlaFra) to $6.3 \pm 0.9\%$ (GraFra; Fig. 2c). Seedling pathogen infestation and seedling herbivory did not correlate (Spearman's $\rho = 0.075$, $P = 0.73$).

Average pathogen infestation of saplings was 6.7% (range: 0–55.5%). Pathogen infestation of saplings was neither affected by fragment quality nor by matrix habitat (Table 1). Sapling pathogen infestation ranged from $3.6 \pm 0.6\%$ (AgrFra) to $7.7 \pm 2.3\%$ (ForFra; Fig. 2c). Sapling pathogen infestation was not correlated with sapling herbivory (Spearman's $\rho = 0.021$, $P = 0.92$). Pathogen infestation of saplings correlated with that of seedlings (Spearman's $\rho = 0.48$, $P = 0.018$).

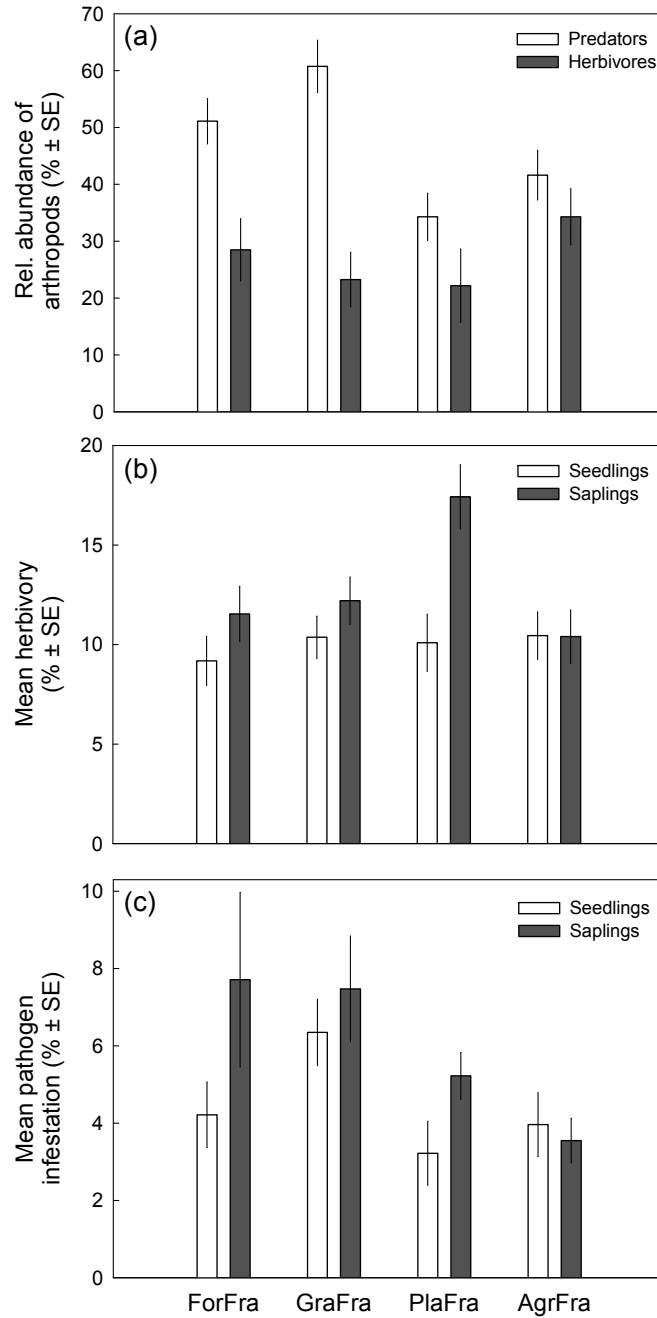


Figure 4.2. Arthropods and leaf damage in response to matrix habitat. Mean percentages (\pm SE) of (a) relative abundances of arthropod predators and herbivores, (b) herbivory on seedlings and saplings and (c) pathogen infestation on seedlings and saplings in large natural forest fragments with forest matrix (ForFra), small natural forest fragments surrounded by grassland (GraFra) and in small modified forest fragments surrounded by plantations (PlaFra) and agriculture (AgrFra). Light bars = arthropod predators, seedlings; dark bars = arthropod herbivores, saplings.

Discussion

Forest fragment quality strongly affected arthropod communities with vegetation complexity increasing predator and canopy cover decreasing herbivore abundance. Furthermore, herbivory of tree recruits showed contrasting responses to forest fragment quality. Seedling herbivory decreased with tree diversity, while sapling herbivory increased. In contrast, canopy cover intensified both, seedling and sapling herbivory. Pathogens were not affected by forest fragment quality. Generally, matrix habitat showed no strong effects on arthropods and leaf damage. Merely, seedling pathogen infestation and sapling herbivory slightly varied with matrix habitat.

FOREST FRAGMENT QUALITY. As expected, forest fragment quality enhanced predator and reduced herbivore abundance. This response, however, was not caused by tree diversity, which would have been in accordance with the ‘enemies hypothesis’ (Root 1973). The hypothesis predicts an increase of predators with higher tree diversity as a result of the concurrently higher structural complexity in diverse systems. Yet, in forests, diversity-predator relationships have been reported to be diverging or to depend on tree species identity (Kaitaniemi *et al.* 2007; Sobek *et al.* 2009; Schuldt *et al.* 2011). In our case, vegetation complexity increased predator and canopy cover decreased herbivore abundance. As tree diversity and vegetation cover were slightly correlated, the structural complexity argument of the ‘enemies hypothesis’ might not be contradicted. The increase of predator abundance with higher habitat complexity is in line with a meta-analytical synthesis by Langellotto and Denno (2004). Thus, in our community-wide approach, structural components of the habitat, such as vegetation complexity and canopy cover, seem to be more important for arthropod abundances than tree diversity *per se*. Moreover, predator-herbivore interactions are difficult to disentangle in diverse, structurally complex habitats as, *e.g.* cover or food may be equally provided or reduced for both (Schmidt & Rypstra 2010).

Responses of herbivory on tree recruits were contrasting with tree diversity decreasing seedling, but increasing sapling herbivory and canopy cover increasing herbivory in both recruitment stages. Matching our expectation as well as arthropod responses to forest fragment quality, seedling herbivory decreased in response to increasing tree diversity. The

result is in line with the concept of 'associational resistance' expecting a reduction of herbivory in diverse systems (Tahvanai & Root 1972; Root 1973) and corresponds to findings of many others (*e.g.* Massey *et al.* 2006; Unsicker *et al.* 2006; Jactel & Brockerhoff 2007). Yet, resource concentration (diversity inhibits host-finding) might be inappropriate to explain responses of seedling herbivory to tree diversity. Firstly, host-specificity might not play a pivotal role for such young seedlings as plant tissue is still soft and might be equally palatable and attractive for many herbivores. Secondly, sapling herbivory increased with higher tree diversity, in contrast to herbivory on seedlings. Such a positive diversity-herbivory relationship has been attributed to higher dietary choice for generalist herbivores and thus a spillover from preferred host plants to adjacent non-host plants ('associational susceptibility', White & Whitham 2000). This supports the idea that our herbivore community consisted of generalist herbivores rather than specialists and that herbivory on tree recruits was not shaped by resource concentration or host-specificity, which refers to specialists.

One possible reason for contrasting responses of arthropods and herbivory to forest fragment quality might be rather weak trophic relationships in forest fragments between arthropod predators and herbivores. These 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 thus 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). Moreover, changes in plant species composition appear possible. There has been evidence that plant palatability is higher in light-demanding than in shade-tolerant species (Ruiz-Guerra *et al.* 2010). Supporting this, sapling herbivory was by trend highest in PlaFra. This fragment type has been shown to consist of a higher proportion of light-demanding tree species compared to the other fragment types in further studies (see chapter 3). Alternatively, other herbivores, not

assessed in the study, such as mammals, appear possible as their abundance might have been connected to closed canopy cover where herbivory on tree recruits was highest.

None of the forest fragment quality measures affected pathogen infestation of seedlings and saplings. This could be explained by the fact that pathogens are highly host-specific making their responses to forest fragment quality difficult to predict (Burdon 1993). Yet, pathogen infestation of seedlings and saplings correlated and were therefore possibly shaped by similar parameters. Seedling pathogen infestation slightly increased with the number of seedling leaves. Young seedlings with fewer leaves seem to be less likely to be infested, while older seedlings with more leaves might have a higher chance of being infested. This might simply be a time effect as it was absent for saplings. As saplings all tend to have more leaves, pathogens might have enough time for infestation. Plant-pathogen interactions, however, seem to be complex and require further studies elucidating their response to forest fragment quality.

MATRIX HABITAT. In accordance with our expectation, we found a slight trend of higher predator abundance in forest fragments within natural heterogeneous surroundings than in fragments with modified homogenous matrix habitat. Similarly, Steffan-Dewenter (2003) also found an increase of predator species with landscape diversity in the matrix. This is in line with the 'trophic rank hypothesis' predicting that higher trophic levels are more susceptible to disturbances (Krüss & Tschardtke 1994; Holt *et al.* 1999). Matrix habitat had no effect on herbivores and sapling herbivory only slightly varied with matrix habitat. This agrees with 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 herbivores and hence herbivory. Likewise, Haynes and Crist (2009) reported neither an effect of matrix composition, nor of fragmentation on insect herbivory.

As the effect of the matrix habitat on predators was considerably weak, we assume that neither predator, nor herbivore dispersal were strongly hampered by matrices surrounding forest fragments. This suggests that the arthropod communities rather consisted of generalist species that may benefit from a diverse matrix with a higher dietary mixture (Unsicker *et al.* 2008; Haynes & Crist 2009). Therefore, even structurally homogenous

matrices might provide exchange of generalist arthropods among scarp forest fragments causing similar herbivory on tree recruits.

Pathogen infestation of seedlings slightly varied with matrix habitat, while pathogen infestation of saplings showed no response. As pathogens are mainly influenced by the spatial pattern of their host and vector species, pathogen responses to variable matrix habitat are difficult to predict (Holdenrieder *et al.* 2004). On one hand changed environmental conditions can increase host tree susceptibility to disease, but on the other hand fragmentation might also hinder pathogen dispersal at a landscape scale (Jules *et al.* 2002; Perkins & Matlack 2002). Consequently, further research should focus on specific interactions between host, vector and pathogen species as all of them might differ in their sensitivity to fragmented landscapes.

Conclusions

In sum, abundances of arthropod predators and herbivores as well as insect herbivory on tree recruits appeared to be rather shaped by forest fragment quality than by matrix habitat. In accordance with our expectations, forest fragment quality increased predator and decreased herbivore abundance. Responses of herbivory to forest fragment quality were variable: closed canopy cover enhanced both seedling and sapling herbivory, whereas higher tree diversity revealed contrasting results, *i.e.* reduced seedling and amplified sapling herbivory. Generally, matrix habitat effects were negligible. Therefore, we assume trophic interactions between arthropod predators, herbivores and herbivory to be weak and diffuse in scarp forest fragments. We suspect differences in herbivore species compositions and plant palatability to be responsible for contrasting effects of forest fragment quality on arthropods and herbivory. Possibly, in-depth studies focussing on species identities and functional roles of arthropods might help explain this mismatch. Pathogen infestation patterns were not affected by any of the measured variables and seemed to be complex and unpredictable. Further research applying elaborate enclosure experiments might clarify the complex interactions of arthropods for seedling and sapling herbivory in forest fragments.

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5 General conclusions

Human-induced land-use change and agricultural intensification entail the formation of mosaic landscapes with fragmented forest embedded in matrix habitat. This in turn may cause fundamental changes in forest regeneration processes, such as seed predation, establishment of woody seedlings and saplings and herbivory. In my thesis, I investigated the influence of forest fragment quality and matrix habitat on biodiversity and ecological processes involved in forest regeneration in a mosaic-forest landscape in KwaZulu-Natal, South Africa.

Elevated seed predation in small forest fragments embedded in high-contrast matrices

In a first approach, I assessed the influence of forest fragment quality and matrix habitat on rodent seed predators and the process of seed predation. As a measure of fragment quality, I estimated herbal ground vegetation cover, which has been shown to affect rodents and seed predation. I compared rodent abundance, species richness and community composition as well as seed predation between large scarp forest fragments with natural forest matrix and three small forest fragments surrounded by natural grassland, eucalypt plantations and sugarcane agriculture. To do so, I trapped rodents with pitfall traps, drift fences and baited Sherman-live traps and conducted seed predation experiments with peanuts inside and outside rodent enclosures. My findings suggest that rodents were important drivers of seed predation in small fragments. This could be explained by increased ground vegetation cover in small forest fragments providing shelter and resources for rodents. Rodent abundance and species richness as well as seed predation were higher in small forest fragments than in large forest fragments. Yet, significant differences only occurred between large natural forest fragments and modified fragments surrounded by sugarcane agriculture. To conclude, I argue that rodents were primarily regulated bottom-up through higher ground vegetation cover creating beneficial conditions in small forest fragments, which in turn led to enhanced seed predation. However, a lack of top-down control of rodents in fragments surrounded by sugarcane due to low matrix permeability for predators appears possible. Consequently, seed survival might be hampered in small scarp forest fragments with possible consequences for forest regeneration.

Late-successional tree recruits decrease in forest fragments with modified matrices

In a second approach, I investigated the effects of scarp forest fragment quality and matrix habitat on natural tree recruitment. I considered three measures of forest fragment quality that might affect the establishment of woody seedlings and saplings, *i.e.* canopy cover, light intensity on the forest floor and vegetation complexity. I determined species richness, abundance and community composition of trees and woody seedlings and saplings in two forest fragment types with natural heterogenous surroundings (forest, grassland) as well as in two forest fragment types with modified homogenous matrix habitat (eucalypt plantations, sugarcane agriculture). To be able to detect shifts in the proportion of early- and late-successional species, I categorized all three stage classes according to their successional status. Moreover, I distinguished between recruitment originating from local and external seed influx depending on the presence of conspecific adult trees within the study plot. Tree communities exhibited reduced species richness and abundance of late-successional species in modified forest fragments surrounded by plantations. Early-successional seedling and sapling species richness and abundance were enlarged at the expense of late-successional species in fragment types with modified matrix habitat, which was supported by multivariate community composition analysis. This shift in successional status in forest fragments with modified matrices was seemingly due to changes in forest fragment quality, such as reduced canopy cover as well as higher light intensity. The decline of late-successional tree recruits in forest fragments surrounded by modified homogenous matrix habitat might indicate impeded forest regeneration potential in these fragments. However, recruitment from external seed influx occurred in all forest fragments suggesting a comparably high permeability of all matrix habitat types for seed dispersers. To conclude, the forest mosaic landscape seemed to sustain connectivity via present external seed influx. Yet, shifts in community composition indicated the high value of natural forests, which can serve as a pool for late-successional species. In consequence, conservation management needs to place the focus on facilitating connectivity across remnant natural forest habitat.

Forest fragment quality rather than matrix habitat shapes herbivory on tree recruits

In a third approach, I quantified the impact of forest fragment quality as well as of matrix habitat on arthropods and leaf damage on tree recruits. Therefore, I assessed forest fragment quality in terms of tree diversity, vertical vegetation complexity and canopy cover. I compared arthropod predator and herbivore abundances, insect herbivory and pathogen infestation on woody seedlings and saplings between forest fragments with two natural heterogeneous (forest, grassland) and two modified homogeneous (eucalypt plantations, sugarcane agriculture) matrix habitat types. Forest fragment quality affected arthropods as vegetation complexity increased predator and canopy cover decreased herbivore abundance. Influence of fragment quality on herbivory was contrasting. Tree diversity reduced seedling, but intensified sapling herbivory. Canopy cover amplified herbivory of both woody seedlings and saplings. Diverging responses of arthropods and herbivory to forest fragment quality might be explained by weak trophic interactions. Moreover, differing herbivore species compositions and plant palatability in forest fragments appear possible. Pathogen infestation was not impacted by forest fragment quality. In general, matrix habitat did not show strong effects on arthropods and leaf damage, as only seedling pathogen infestation and sapling herbivory tended to vary with matrix habitat. This suggests similarly high matrix permeability for arthropods. Concluding, arthropods and insect herbivory on tree recruits seemed to be influenced by forest fragment quality rather than by matrix habitat while pathogen responses to forest fragmentation seemed to be complex and difficult to predict. Further research, possibly by means of enclosure experiments, might help to disentangle the effects of fragmentation on trophic interactions among arthropods and plants.

Synthesis

Overall, my results illustrate that forest fragment quality as well as matrix habitat have the potential to alter biodiversity and ecological processes involved in forest regeneration. However, the different communities and processes I studied reacted variably to forest fragment quality and matrix habitat. This variability might be caused by diverging traits

inherent to the different species groups involved, *e.g.* different habitat requirements, biotic interactions with other species or dispersal abilities. For instance, higher ground vegetation cover favoured rodents by providing resources and shelter. Moreover, rodents were potentially ecologically released from top-down control of predators in small fragments. This indicates that rodent seed predators might be strongly affected by both vegetation and trophic interactions. In contrast, woody seedlings and saplings appeared to be rather influenced by abiotic factors, such as canopy cover and light intensity. Further, arthropod communities were seemingly shaped by vegetation characteristics whereas trophic interactions appeared to be of minor relevance. In conclusion, this highlights the importance of investigating not only exemplary processes, but also the complex interplay of several processes to really fully understand the consequences of forest fragmentation and matrix habitat for regeneration.

In sum, the effects of forest fragment quality and matrix habitat on the ecological processes of seed predation, establishment of woody seedlings and saplings as well as on herbivory differed in strength. Yet, I generally found that forest fragment quality appears to be of high relevance for regeneration, indicating its potential for conservation management of the remaining fragments. Further, the rather weak overall effects of matrix habitat indicate a comparable and generally high permeability for the investigated groups of species. This emphasizes the significant value of forest fragments for the connectivity of remaining forests and the conservation of biodiversity and ecological processes at a landscape scale. Nevertheless, conclusions have to be treated with care. Due to the historical natural fragmentation of scarp forests in KwaZulu-Natal, which might have caused a higher resistance of species towards human-induced fragmentation, my findings might not be transferable to other regions. The scarp forest fragments are indeed characterized by high habitat quality for the different species groups. However, potential shifts in the plant community from late- to early-successional species in fragments enclosed by modified matrices might entail unforeseen cascading effects and negative feedback loops within the ecosystem that still need to be examined. Thus, the value of natural forest as a source of propagules and as habitat for forest specialists remains indisputable.

FURTHER RESEARCH OPTIONS. My studies showed that forest regeneration processes in human-modified landscapes seem to be highly complex. All three studies were of exemplary character and effect sizes were rather weak, thus making it difficult to draw strong conclusions. In part, this might be attributed to the historical fragmentation of the landscape since the last glacial maximum. Further research has to clarify if historical confrontation with natural disturbances entails higher resistance of ecosystems when exposed to human impact (*e.g.* Lawes *et al.* 2005). Furthermore, investigations of species-specific matrix permeability and landscape connectivity are scarce. Future studies should combine sampling of different taxa within natural forest, forest fragments, at forest edges and –most frequently ignored– within matrices themselves. Moreover, species occurrence data often reflect only a ‘snapshot’ of actual population dynamics. This emphasizes the need for long-term monitoring to assess population viability in modified landscapes (*e.g.* Sekercioglu *et al.* 2007). In this context, movement data, *e.g.* from transmitters fitted onto birds or even propagules, such as seeds may provide a deeper understanding of species behavioural responses to landscape modification (*e.g.* Jansen *et al.* 2004; Lenz *et al.* 2011).

Lastly, determining species identities and functions is essential for linking biodiversity directly to ecological processes. This might be achieved through *e.g.* the use of camera traps, which could be valuable to identify seed predators (*e.g.* Iob & Vieira 2008). Additionally, a link between species and their function could be acquired through experimental studies, such as feeding experiments with *e.g.* rodents and seeds (*e.g.* Farwig *et al.* 2008a) or enclosure experiments with arthropod predators, herbivores and plants (*e.g.* Böhm *et al.* 2011). Further, genetic parentage analyses may assist in tracing back seeds to adult trees allowing estimates on dispersal distances and the origin of seed influx (*e.g.* Grivet *et al.* 2005). Moreover, extending investigations from the species-level to a community perspective, *e.g.* through the investigation of community-wide interaction networks (*e.g.* Bascompte & Jordano 2007), could reveal a more comprehensive understanding of the functioning of modified ecosystems. Overall, applying these approaches may be valuable to further elucidate the persistence of biodiversity and related ecosystem processes in human-modified and fragmented forest landscapes.

6 Future challenges for conservation in mosaic-forest landscapes

My study shows that non-protected small forest fragments within human-modified matrices can to a certain degree assist to maintain biodiversity and ecological processes at a landscape scale. This is a contribution to the currently pressing question on how to succeed in conserving biodiversity in a human-modified world. The continuously growing human population and its need for food has led to a heated debate on how to globally integrate food production and biodiversity conservation as both compete for space (Fischer *et al.* 2011; Phalan *et al.* 2011). One concept—‘land sparing’—is to separate strictly protected areas for conservation from intensive high-yield agriculture for food production (Phalan *et al.* 2011). The other idea—called ‘land sharing’—favours uniting both approaches on the same land by using farming techniques that contribute to biodiversity conservation, such as agroforestry (*e.g.* Perfecto & Vandermeer 2010). While Phalan *et al.* (2011) recently demonstrated that land sparing seems to be the better option for most investigated bird and tree species both in Ghana and India, others argue that high agricultural yield and high biodiversity are not mutually exclusive (*e.g.* Clough *et al.* 2011).

As about 40% of the land surface is already used for agriculture or pasture, the concept of purely natural systems has potentially become obsolete in most regions of the world (Foley *et al.* 2005). Moreover, the long-term viability of protected areas might be questionable as they are often isolated within modified landscapes and highly exposed to human activities in their adjacency (Wittemyer *et al.* 2008). Of course, protected areas and old-growth forests are undoubtedly necessary for habitat specialists, *e.g.* for late-successional tree species or for animals with large home ranges (Gibson *et al.* 2011). However, biodiversity conservation in our human-modified world cannot only rely on protected areas (*e.g.* Rodrigues *et al.* 2004). Therefore, one of the biggest challenges for today’s conservation scientists is to develop an integrated conservation management approach that involves both human and ecological factors across the entire landscape mosaic (Gardner *et al.* 2009; Perfecto & Vandermeer 2010; Fischer *et al.* 2011).

To take up this challenge, we need to discover to what extent species can persist in modified landscapes, identify their individual habitat requirements and their dispersal limitations (Gardner *et al.* 2009). It is therefore essential to estimate the value of modified landscapes for different taxa. My results demonstrate that either structural characteristics, *e.g.* forest fragment quality or the matrix habitat might determine the persistence of different groups of species and ecological processes. Thus, taking into account that human-modified

landscapes are often spatially heterogenous, *i.e.* contain a high variety of forest cover types, the question above calls for applicable measures of landscape heterogeneity to quantify a landscape's suitability for ecosystem conservation. As an example, the measure of 'functional landscape heterogeneity' seems to be a promising tool to integrate highly variable species requirements at a landscape scale (Fahrig *et al.* 2011). Thereby, specific heterogeneity criteria for different species groups, *e.g.* floristic composition for insects or nesting sites for birds are considered (Fahrig *et al.* 2011). Moreover, as the persistence of populations in human-modified landscapes has been shown to depend on their ability to move across the entire mosaic (Tewksbury *et al.* 2002), we need to develop and evaluate strategies that aim at providing connectivity for different species through, *e.g.* corridors or live fences. Most likely, the combination of both land-sparing for protected areas and land-sharing along with improving the quality of the landscape for many taxa will yield the highest conservation success.

Lastly, modified landscapes are characterized by social-ecological dynamics that often determine success or failure of conservation strategies (Liu *et al.* 2007). This emphasizes the need to follow context-dependent multidisciplinary or even transdisciplinary and participatory approaches in collaborative research projects that involve all relevant stakeholders (Barlow *et al.* 2011). These could be ecologists, social scientists, conservationists, indigenous peoples, rural social movements, farmers, land owners, tourists, politicians, land managers as well as representatives from different administrative boards, *i.e.* agriculture, water management and forestry (Chazdon *et al.* 2009). Only then, we might succeed in developing a holistic perspective on land use and landscape management that will help to create sustainable conservation strategies and policies.

7 Deutsche Zusammenfassung

Weltweit werden Wälder in alarmierender Geschwindigkeit zerstört und fragmentiert. Landschaften bestehen zunehmend aus Mosaiken mit Waldfragmenten in variablem Matrixhabitat. Es ist daher essentiell zu verstehen, inwiefern diese Habitatveränderungen die Funktion und Stabilität von Waldökosystemen beeinflussen. Die komplexen Zusammenhänge zwischen anthropogener Störung von Wäldern, dem dadurch bedingten Artenverlust und den betroffenen Ökosystemfunktionen sind jedoch nach wie vor nicht hinreichend geklärt.

In der vorliegenden Arbeit untersuchte ich die Einflüsse von Waldfragmentqualität und Matrixhabitat auf Biodiversität und ökologische Prozesse der Waldregeneration. Zu diesem Zweck führte ich drei exemplarische Feldstudien in einer fragmentierten Waldlandschaft in KwaZulu-Natal, Südafrika durch. Ich erfasste 1) Samenprädation durch Nager, 2) Etablierung von Baumkeimlingen und -schösslingen sowie 3) Blattschäden an Baumkeimlingen und -schösslingen durch Insekten und Pathogene auf 24 Untersuchungsflächen in Fragmenten so genannter Hangwälder („scarp forests“). Diese Waldfragmente waren von vier verschiedenen Matrixhabitaten umgeben. Fragmente innerhalb der Naturreservate Vernon Crookes und Oribi Gorge wiesen natürliche und strukturell heterogene Matrices auf (Wald, Grassland); Fragmente in direkter Nachbarschaft der Naturreservate waren von modifizierten und strukturell homogenen Matrices umgeben (Eukalyptus-Plantagen, Zuckerrohrfelder).

Für die erste Studie nahm ich die Nagerdiversität mithilfe von Eimerfallen und beköderten Lebendfallen über drei Tage hin auf. Ferner führte ich Samenprädationsexperimente durch, indem ich Erdnüsse innerhalb und außerhalb von Nager-Ausschlusskäfigen platzierte und ebenfalls über drei Tage die Fraßrate ermittelte. Zudem schätzte ich als Maß für die Waldfragmentqualität die Bodenbedeckung durch krautige Pflanzen, da diese für Nager eine wichtige Rolle spielt. Für die zweite Studie bestimmte ich die Baumdiversität aller adulten Bäume auf 500 m² pro Untersuchungsfläche, die Keimlingsdiversität auf 10 m² und die Schösslingsdiversität auf 50 m². Um Veränderungen in der Artenzusammensetzung feststellen zu können, unterteilte ich Bäume, Keimlinge und Schösslinge nach ihrem Sukzessionsstatus in Pionier- und Klimaxarten. Des Weiteren differenzierte ich zwischen Keimlingen und Schösslingen mit externer und lokaler Herkunft, abhängig von der Präsenz artgleicher adulter Bäume im Fragment, um so auf eventuellen Sameneintrag durch Samenausbreiter rückschließen zu können. Außerdem

nahm ich Kronenbedeckung, Lichtintensität und Vegetationskomplexität als für die Etablierung von Keimlingen relevante Parameter der Waldfragmentqualität auf. Für die dritte Studie ermittelte ich mithilfe eines Klopfschirms die Arthropoden-Prädatoren- und Arthropoden-Herbivoren-Gemeinschaft in den Waldfragmenten. Zusätzlich schätzte ich den prozentualen Blattschaden durch Insektenherbivorie und Pathogenbefall an Baumkeimlingen und -schösslingen. Bezüglich der Fragmentqualität nahm ich die Diversität adulter Bäume, Kronenbedeckung und Vegetationskomplexität auf.

Meine Untersuchungen deuteten auf ein erhöhtes Nagervorkommen und dadurch verstärkte Samenprädation in kleinen Waldfragmenten hin, was vermutlich mit der höheren Bodenbedeckung an krautigen Pflanzen zusammenhing. Speziell in Fragmenten im Zuckerrohr waren Nagervorkommen und Samenprädation signifikant höher als in Fragmenten mit Waldmatrix. Ferner konnte ich eine reduzierte Keimlings- und Schösslingsetablierung in den Waldfragmenten mit modifizierten homogenen Matrices feststellen. Im Besonderen kam es zu einer Verringerung von Klimaxarten in diesen Fragmenten. Dies wurde hauptsächlich durch abnehmende Kronenbedeckung mit einhergehender erhöhter Lichtintensität bedingt. Jedoch fand externer Sameneintrag in allen Waldfragmenten statt, was auf die Durchlässigkeit der Matrix für Samenausbreiter hindeutete. Des Weiteren kam es zu einem Anstieg an Arthropoden-Prädatoren und einem Rückgang an Arthropoden-Herbivoren mit zunehmender Fragmentqualität. Der Einfluss der Waldfragmentqualität auf Herbivorie war variabel. Diese Abweichungen könnten mit schwachen trophischen Interaktionen zusammenhängen. Ferner waren möglicherweise Unterschiede in der Artenzusammensetzung der Herbivoren oder in der Annehmbarkeit der Pflanzen für Herbivoren verantwortlich für konträre Effekte der Fragmentqualität auf Arthropoden und Herbivorie. Das Matrixhabitat hatte nur marginale Effekte auf die untersuchten Faktoren.

Insgesamt zeigen meine Ergebnisse, dass Waldfragmentqualität und Matrixhabitat Biodiversität und ökologische Prozesse der Waldregeneration beeinflussen. Die Effekte auf Samenprädation, Keimlings- und Schösslingsetablierung sowie Herbivorie waren dabei unterschiedlich. Generell schien die Fragmentqualität jedoch eine wichtige Bedeutung für die Waldregeneration zu haben, was ihr Potential für Naturschutzmaßnahmen in den Fragmenten hervorhebt. Ferner lassen die schwachen Effekte der variablen Matrices in unserem Untersuchungsgebiet eine vergleichbar hohe Durchlässigkeit für die untersuchten

Artengruppen erkennen. Das unterstreicht den Wert der Waldfragmente als Habitatinselfeln in modifizierten Landschaften und für den Erhalt von Biodiversität und ökologischen Prozessen auf der Landschaftsebene. Nichtsdestotrotz ist bei der Verallgemeinerung der Aussagen Vorsicht angebracht. Aufgrund der historisch bedingten natürlichen Fragmentierung der Hangwälder in KwaZulu-Natal, die zu einer hohen Resistenz der Artengruppen gegenüber menschlich verursachter Waldfragmentierung beigetragen haben könnte, sind die Ergebnisse nur eingeschränkt auf andere Regionen übertragbar. Die Fragmente zeichnen sich zwar durch ihre hohe Habitatqualität für verschiedene Artengruppen aus, jedoch könnten die Verschiebungen in den Pflanzengemeinschaften von Klimax- zu Pionierarten in Waldfragmenten mit modifizierten Matrices unvorhersehbare Kaskadeneffekte mit sich bringen. Das macht den Erhalt von großen zusammenhängenden Wäldern als Quelle für Klimaxarten und Habitat für spezialisierte Arten unerlässlich.

8 References

- Asquith, N. M., Wright, S. J., and Clauss, M. J. (1997). Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. *Ecology* 78, 941–946.
- Babaasa, D., Eilu, G., Kasangaki, A., Bitariho, R., and McNeilage, A. (2004). Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 42, 217–224.
- Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., and Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9, 1146–1156.
- Barlow, J., Ewers, R. M., Anderson, L., Aragao, L. E. O. C., Baker, T. R., Boyd, E., Feldpausch, T. R., Gloor, E., Hall, A., Malhi, Y., Milliken, W., Mulligan, M., Parry, L., Pennington, T., Peres, C. A., Phillips, O. L., Roman-Cuesta, R. M., Tobias, J. A., and Gardner, T. A. (2011). Using learning networks to understand complex systems: a case study of biological, geophysical and social research in the Amazon. *Biological Reviews* 86, 457–474.
- Bascompte, J. and Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38, 587–593.
- Bender, D. J. and Fahrig, L. (2005). Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86, 1023–1033.
- Benítez-Malvido, J. (1998). Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12, 380–389.
- Benítez-Malvido, J., García-Guzmán, G., and Kossmann-Ferraz, I. D. (1999). Leaf-fungal incidence and herbivory on tree seedlings in tropical rainforest fragments: an experimental study. *Biological Conservation* 91, 143–150.

- Benítez-Malvido, J. and Lemus-Albor, A. (2005). The seedling community of tropical rain forest edges and its interaction with herbivores and pathogens. *Biotropica* 37, 301–313.
- Benítez-Malvido, J. and Martínez-Ramos, M. (2003a). Impact of forest fragmentation on understory plant species richness in Amazonia. *Conservation Biology* 17, 389–400.
- Benítez-Malvido, J. and Martínez-Ramos, M. (2003b). Influence of edge exposure on tree seedling species recruitment in tropical rain forest fragments. *Biotropica* 35, 530–541.
- Bennett, A. F., Radford, J. Q., and Haslem, A. (2006). Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation* 133, 250–264.
- Bernard, H., Fjeldsa, J., and Mohamed, M. (2009). A case study on the effects of disturbance and conversion of tropical lowland rain forest on the non-volant small mammals in North Borneo: management implications. *Mammal Study* 34, 85–96.
- Bibby, C. J., Burgess, N. D., Hill, D. A., and Mustoe, S. H. (2000). Bird census techniques. Academic Press, London.
- Bodin, O., Tengo, M., Norman, A., Lundberg, J., and Elmqvist, T. (2006). The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. *Ecological Applications* 16, 440–451.
- Böhm, S. M., Wells, K., and Kalko, E. K. V. (2011). Top-down control of herbivory by birds and bats in the canopy of temperate broad-leaved oaks (*Quercus robur*). *Plos One* 6, e17857.
- Boon, R. (2010). Pooley's trees of eastern South Africa – a complete guide. Flora and Fauna Publications Trust, Durban.
- Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P., and Sayer, J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* 17, 925–951.

- Burdon, J. J. (1993). The structure of pathogen populations in natural plant-communities. *Annual Review of Phytopathology* 31, 305–323.
- Chao, A. (2005). Species richness estimation. In *Encyclopedia of Statistical Sciences*. Eds N. Balakrishnan, C. B. Read, and B. Vidakovic. pp. 7909–7916. Wiley, New York.
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., and Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14, 922–932.
- Chazdon, R. L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology Evolution and Systematics* 6, 51–71.
- Chazdon, R. L., Harvey, C. A., Komar, O., Griffith, D. M., Ferguson, B. G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., van Breugel, M., and Philpott, S. M. (2009). Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica* 41, 142–153.
- Clough, Y., Barkmann, J., Juhbandt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D. D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C. H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., Wielgoss, A. C., and Tschardtke, T. (2011). Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America* 108, 8311–8316.
- Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Krüss, A., Steffan-Dewenter, I., and Tschardtke, T. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology* 44, 804–812.
- Coates Palgrave, M. (2005). *Keith Coates Palgrave trees of southern Africa*. Struik Publishers, Cape Town.

- Cole, R. J. (2009). Postdispersal seed fate of tropical montane trees in an agricultural landscape, Southern Costa Rica. *Biotropica* 41, 319–327.
- Colwell, R. K. (2009) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at <http://purl.oclc.org/estimates>.
- Colwell, R. K. and Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 345, 101–118.
- Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations*. Eds P. J. Den Boer and G. R. Gradwell. pp. 298–312. Pudoc, Wageningen.
- Cooper, K. H. (1985). The conservation status of indigenous forests in Transvaal, Natal and O.F.S., South Africa. Wildlife Society of South Africa, Durban.
- Cordeiro, N. J. and Howe, H. F. (2001). Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* 15, 1733–1741.
- Cordeiro, N. J., Ndangalasi, H. J., McEntee, J. P., and Howe, H. F. (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90, 1030-1041.
- Crist, T. O., Veech, J. A., Gering, J. C., and Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: A hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* 162, 734–743.
- Daily, G. C. (2001). Ecological forecasts. *Nature* 411, 245.
- Daily, G. C., Ceballos, G., Pacheco, J., Suzan, G., and Sanchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17, 1814–1826.

- DeMattia, E. A., Curran, L. M., and Rathcke, B. J. (2004). Effects of small rodents and large mammals on neotropical seeds. *Ecology* 85, 2161–2170.
- Diekötter, T., Haynes, K. J., Mazeffa, D., and Crist, T. O. (2007). Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. *Oikos* 116, 1588–1598.
- Donoso, D. S., Grez, A. A., and Simonetti, J. A. (2003). Effects of forest fragmentation on the granivory of differently sized seeds. *Biological Conservation* 115, 63–70.
- Edwards, M. B. P. and Roberts, P. J. T. (2006). Managing forests for water: the South African experience. *International Forestry Review* 8, 65–71.
- Eeley, H. A. C., Lawes, M. J., and Piper, S. E. (1999). The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography* 26, 595–617.
- Eeley, H. A. C., Lawes, M. J., and Reyers, B. (2001). Priority areas for the conservation of subtropical indigenous forest in southern Africa: a case study from KwaZulu-Natal. *Biodiversity and Conservation* 10, 1221–1246.
- Estrada, A. and Coates-Estrada, R. (2001). Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography* 24, 94–102.
- Estrada, A. and Coates-Estrada, R. (2002). Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 11, 1903–1918.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34, 487–515.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., and Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14, 101–112.

- FAO. (2010) Global Forest Resources Assessment 2010. Food and Agriculture Organization of the United Nations, Rome.
- Farwig, N., Bailey, D., Bochud, E., Herrmann, J. D., Kindler, E., Reusser, N., Schüpp, C., and Schmidt-Entling, M. H. (2009). Isolation from forest reduces pollination, seed predation and insect scavenging in Swiss farmland. *Landscape Ecology* 24, 919–927.
- Farwig, N., Bleher, B., der Gonna, S., and Böhning-Gaese, K. (2008a). Does forest fragmentation and selective logging affect seed predators and seed predation rates of *Prunus africana* (Rosaceae)? *Biotropica* 40, 218–224.
- Farwig, N., Sajita, N., Schaab, G., and Böhning-Gaese, K. (2008b). Human impact diminishes seedling species richness in Kakamega Forest, Kenya. *Basic and Applied Ecology* 9, 383–391.
- Faveri, S. B., Vasconcelos, H. L., and Dirzo, R. (2008). Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *Journal of Tropical Ecology* 24, 57–64.
- Fischer, J., Batory, P., Bawa, K. S., Brussaard, L., Chappell, M. J., Clough, Y., Daily, G. C., Dorrough, J., Hartel, T., Jackson, L. E., Klein, A. M., Kremen, C., Kuemmerle, T., Lindenmayer, D. B., Mooney, H. A., Perfecto, I., Philpott, S. M., Tscharrntke, T., Vandermeer, J., Wanger, T. C., and Von Wehrden, H. (2011). Conservation: limits of land sparing. *Science* 334, 593.
- Fischer, J. and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16, 265–280.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., and Snyder, P. K. (2005). Global consequences of land use. *Science* 309, 570–574.

- Forget, P. M. (1996). Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12, 751–761.
- Forget, P. M. and Cuiljpers, L. (2008). Survival and scatterhoarding of frugivores-dispersed seeds as a function of forest disturbance. *Biotropica* 40, 380–385.
- García, D. and Bañuelos, M. J. (2003). Matrix matters for seed dispersal - a comment to Jules & Shahani. *Journal of Vegetation Science* 14, 931.
- García, D. and Chacoff, N. P. (2007). Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology* 21, 400–411.
- García-Guzmán, G. and Dirzo, R. (2001). Patterns of leaf-pathogen infection in the understory of a Mexican rain forest: Incidence, spatiotemporal variation, and mechanisms of infection. *American Journal of Botany* 88, 634–645.
- Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., and Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12, 561–582.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., and Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–383.
- Gotelli, N. J. and Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4, 379–391.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W., and Balmford, A. (2005). Farming and the fate of wild nature. *Science* 307, 550–555.
- Greenberg, R., Bichier, P., Angon, A. C., MacVean, C., Perez, R., and Cano, E. (2000). The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* 81, 1750–1755.

- Griffiths, M. E., Lawes, M. J., and Tsvuura, Z. (2007). Understorey gaps influence regeneration dynamics in subtropical coastal dune forest. *Plant Ecology* 189, 227–236.
- Grivet, D., Smouse, P. E., and Sork, V. L. (2005). A novel approach to an old problem: tracking dispersed seeds. *Molecular Ecology* 14, 3585–3595.
- Gubista, K. R. (1999). Small mammals of the Ituri Forest, Zaire: Diversity and abundance in ecologically distinct habitats. *Journal of Mammalogy* 80, 252–262.
- Haas, S. E., Hooten, M. B., Rizzo, D. M., and Meentemeyer, R. K. (2011). Forest species diversity reduces disease risk in a generalist plant pathogen invasion. *Ecology Letters* 14, 1108–1116.
- Hagenah, N., Prins, H. H. T., and Olf, H. (2009). Effects of large herbivores on murid rodents in a South African savanna. *Journal of Tropical Ecology* 25, 483–492.
- Haila, Y. (2002). A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12, 321–334.
- Hammond, D. S. (1995). Postdispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. *Journal of Tropical Ecology* 11, 295–313.
- Hanski, I. and Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature* 404, 755–758.
- Harvey, C. A., Medina, A., Sanchez, D. M., Vilchez, S., Hernandez, B., Saenz, J. C., Maes, J. M., Casanoves, F., and Sinclair, F. L. (2006). Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications* 16, 1986–1999.
- Hay, M. E. and Fuller, P. J. (1981). Seed escape from heteromyid rodents - the importance of microhabitat and seed preference. *Ecology* 62, 1395–1399.

- Haynes, K. J. and Crist, T. O. (2009). Insect herbivory in an experimental agroecosystem: the relative importance of habitat area, fragmentation, and the matrix. *Oikos* 118, 1477–1486.
- Haynes, K. J., Diekötter, T., and Crist, T. O. (2007). Resource complementation and the response of an insect herbivore to habitat area and fragmentation. *Oecologia* 153, 511–520.
- Herrera, J. M. and García, D. (2009). The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation* 142, 149–158.
- Herrera, J. M., García, D., and Morales, J. M. (2011). Matrix effects on plant-frugivore and plant-predator interactions in forest fragments. *Landscape Ecology* 26, 125–135.
- Holdenrieder, O., Pautasso, M., Weisberg, P. J., and Lonsdale, D. (2004). Tree diseases and landscape processes: the challenge of landscape pathology. *Trends in Ecology & Evolution* 19, 446–452.
- Holt, R. D., Lawton, J. H., Polis, G. A., and Martinez, N. D. (1999). Trophic rank and the species-area relationship. *Ecology* 80, 1495–1504.
- Hoshizaki, K., Suzuki, W., and Sasaki, S. (1997). Impacts of secondary seed dispersal and herbivory on seedling survival in *Aesculus turbinata*. *Journal of Vegetation Science* 8, 735–742.
- Howe, H. F. and Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Hulme, P. E. (1996). Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* 84, 609–615.
- Hulme, P. E. (1998). Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 1, 32–46.

- Hunter, M. D. and Price, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724–732.
- Iob, G. and Vieira, E. M. (2008). Seed predation of *Araucaria angustifolia* (Araucariaceae) in the Brazilian Araucaria Forest: influence of deposition site and comparative role of small and 'large' mammals. *Plant Ecology* 198, 185–196.
- Jactel, H. and Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10, 835–848.
- Jactel, H., Menassieu, P., Vetillard, F., Gaulier, A., Samalens, J. C., and Brockerhoff, E. G. (2006). Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 36, 314–323.
- Jansen, P. A., Bongers, F., and Hemerik, L. (2004). Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* 74, 569–589.
- Jansen, P. A., Bongers, F., and Prins, H. H. T. (2006). Tropical rodents change rapidly germinating seeds into long-term food supplies. *Oikos* 113, 449–458.
- Janssen, A., Sabelis, M. W., Magalhaes, S., Montserrat, M., and Van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology* 88, 2713–2719.
- Janzen, D. H. (1970). Herbivores and number of tree species in tropical forests. *American Naturalist* 104, 501–528.
- Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics* 2, 465–492.
- Jules, E. S., Kauffman, M. J., Ritts, W. D., and Carroll, A. L. (2002). Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. *Ecology* 83, 3167–3181.

- Jules, E. S. and Shahani, P. (2003). A broader ecological context to habitat fragmentation: why matrix habitat is more important than we thought. *Journal of Vegetation Science* 14, 459–464.
- Kaitaniemi, P., Riihimäki, J., Koricheva, J., and Vehviläinen, H. (2007). Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fennica* 41, 259–268.
- Kalka, M. B., Smith, A. R., and Kalko, E. K. V. (2008). Bats limit arthropods and herbivory in a tropical forest. *Science* 320, 71.
- Kariuki, M. and Kooyman, R. M. (2005). Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* 30, 844–855.
- Keesing, F., Belden, L. K., Daszak, P., Dobson, A., Harvell, C. D., Holt, R. D., Hudson, P., Jolles, A., Jones, K. E., Mitchell, C. E., Myers, S. S., Bogich, T., and Ostfeld, R. S. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468, 647–652.
- Kirika, J. M., Böhning-Gaese, K., Dumbo, B., and Farwig, N. (2010). Reduced abundance of late-successional trees but not of seedlings in heavily compared with lightly logged sites of three East African tropical forests. *Journal of Tropical Ecology* 26, 533–546.
- Krüss, A. and Tscharntke, T. (1994). Habitat Fragmentation, Species Loss, and Biological-Control. *Science* 264, 1581–1584.
- Kupfer, J. A., Malanson, G. P., and Franklin, S. B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15, 8–20.
- Lambert, T. D., Malcolm, J. R., and Zimmerman, B. L. (2005). Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed

- predation in the southeastern Amazon basin. *Forest Ecology and Management* 206, 381–398.
- Langellotto, G. A. and Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139, 1–10.
- Laurance, W. F., Camargo, J. L. C., Luizao, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Williamson, G. B., Benítez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A., and Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* 144, 56–67.
- Laurance, W. F., Ferreira, L. V., Rankin-De Merona, J. M., Laurance, S. G., Hutchings, R. W., and Lovejoy, T. E. (1998). Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460–464.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G., and Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16, 605–618.
- Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., and Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482.
- Lawes, M. J. (1990). The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* Geoffroy, I., 1843) and forest history in southern Africa. *Journal of Biogeography* 17, 669–680.
- Lawes, M. J., Joubert, R., Griffiths, M. E., Boudreau, S., and Chapman, C. A. (2007). The effect of the spatial scale of recruitment on tree diversity in Afromontane forest fragments. *Biological Conservation* 139, 447–456.

- Lawes, M. J., Lamb, B. C. C., and Boudreau, S. (2005). Area- but no edge-effect on woody seedling abundance and species richness in old Afromontane forest fragments. *Journal of Vegetation Science* 16, 363–372.
- Lei, T. T., Semones, S. W., Walker, J. F., Clinton, B. D., and Nilsen, E. T. (2002). Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. *International Journal of Plant Sciences* 163, 991–1000.
- Leibold, M. A., Chase, J. M., Shurin, J. B., and Downing, A. L. (1997). Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28, 467–494.
- Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B. H., Wikelski, M., and Böhning-Gaese, K. (2011). Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proceedings of the Royal Society B-Biological Sciences* 278, 2257–2264.
- Lindenmayer, D. B. and Hobbs, R. J. (2004). Fauna conservation in Australian plantation forests - a review. *Biological Conservation* 119, 151–168.
- Liu, J. G., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., Pell, A. N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C. L., Schneider, S. H., and Taylor, W. W. (2007). Complexity of coupled human and natural systems. *Science* 317, 1513–1516.
- MacArthur, R. and Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Maron, J. L. and Crone, E. (2006). Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B-Biological Sciences* 273, 2575–2584.
- Martínez-Ramos, M. and Soto-Castro, A. (1993). Seed rain and advanced regeneration in a tropical rain-forest. *Vegetatio* 108, 299–318.

- Massey, F. P., Massey, K., Press, M. C., and Hartley, S. E. (2006). Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. *Journal of Ecology* 94, 646–655.
- McCann, K., Hastings, A., and Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature* 395, 794–798.
- MEA (2005) Millenium Ecosystem Assessment. Forest and woodland systems. In Ecosystems and human well-being: current state and trends. Findings of the condition and trends working group. Eds R. Hassan, R. Scholes, and N. Ash. pp. 585–621. Island Press, Washington.
- Melo, F. P. L., Martinez-Salas, E., Benítez-Malvido, J., and Ceballos, G. (2010). Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *Journal of Tropical Ecology* 26, 35–43.
- Mitchell, C. E., Tilman, D., and Groth, J. V. (2002). Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. *Ecology* 83, 1713–1726.
- Montgomery, R. A. and Chazdon, R. L. (2001). Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82, 2707–2718.
- Mortelliti, A. and Boitani, L. (2006). Patterns of rodent species diversity and abundance in a Kenyan relict tropical rainforest. *Biodiversity and Conservation* 15, 1425–1440.
- Murcia, C. (1995). Edge effects in fragmented forests - implications for conservation. *Trends in Ecology & Evolution* 10, 58–62.
- Murphy, H. T. and Lovett-Doust, J. (2004). Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos* 105, 3–14.
- Nascimento, H. E. M., Andrade, A. C. S., Camargo, J. L. C., Laurance, W. F., Laurance, S. G., and Ribeiro, J. E. L. (2006). Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology* 20, 853–860.

- Neuschulz, E. L., Botzat, A., and Farwig, N. (2011). Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. *Oikos* 120, 1371–1379.
- Notman, E. and Gorchoy, D. L. (2001). Variation in post-dispersal seed predation in mature Peruvian lowland tropical forest and fallow agricultural sites. *Biotropica* 33, 621–636.
- Oksanen, J. (2011) Multivariate analysis of ecological communities in R: vegan tutorial. Available at <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. (2011) vegan: Community Ecology Package. Available at <http://CRAN.R-project.org/package=vegan>.
- Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., and Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66, 1–43.
- Pardini, R., Faria, D., Accacio, G. M., Laps, R. R., Mariano-Neto, E., Paciencia, M. L. B., Dixo, M., and Baumgarten, J. (2009). The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* 142, 1178–1190.
- Perfecto, I. and Vandermeer, J. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences of the United States of America* 107, 5786–5791.
- Perkins, T. E. and Matlack, G. R. (2002). Human-generated pattern in commercial forests of southern Mississippi and consequences for the spread of pests and pathogens. *Forest Ecology and Management* 157, 143–154.
- Perrin, M. R. (2002). Space use by a reintroduced serval in Mount Currie Nature Reserve. *South African Journal of Wildlife Research* 32, 79–86.

- Phalan, B., Onial, M., Balmford, A., and Green, R. E. (2011). Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333, 1289–1291.
- Picker, M., Griffiths, C., and Weaving, A. (2004). Field guide to insects of South Africa. Struik Publishers, Cape Town.
- Polis, G. A., Sears, A. L. W., Huxel, G. R., Strong, D. R., and Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15, 473–475.
- Prevedello, J. A. and Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19, 1205–1223.
- R Development Core Team. (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org>.
- R Development Core Team. (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org>.
- Ramírez-Marcial, N. (2003). Survival and growth of tree seedlings in anthropogenically disturbed Mexican montane rain forests. *Journal of Vegetation Science* 14, 881–890.
- Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158, 87–99.
- Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., da Fonseca, G. A. B., Gaston, K. J., Hoffmann, M., Long, J. S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., Watts, M. E. J., and Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature* 428, 640–643.

- Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95–120.
- Roscher, C., Schumacher, J., Foitzik, O., and Schulze, E. D. (2007). Resistance to rust fungi in *Lolium perenne* depends on within-species variation and performance of the host species in grasslands of different plant diversity. *Oecologia* 153, 173–183.
- Ruiz-Guerra, B., Guevara, R., Mariano, N. A., and Dirzo, R. (2010). Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: evidence from a Mexican tropical rain forest. *Oikos* 119, 317–325.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Hünneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Biodiversity - global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Santos, B. A. and Benítez-Malvido, J. (2012). Insect herbivory and leaf disease in natural and human disturbed habitats: lessons from early-successional *Heliconia* herbs. *Biotropica* 44, 53–62.
- Santos, T. and Tellería, J. L. (1994). Influence of forest fragmentation on seed consumption and dispersal of Spanish Juniper *Juniperus thurifera*. *Biological Conservation* 70, 129–134.
- Saunders, D. A., Hobbs, R. J., and Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18–32.
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E. D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A. M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V. D., Milcu, A., Müller, R., Partsch, S., Petermann, J. S.,

- Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V. M., and Tschamntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468, 553–556.
- Schmidt, J. M. and Rypstra, A. L. (2010). Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia* 164, 899–910.
- Scholtz, C. H. and Holm, E. (1985). *Insects of southern Africa*. Butterworths, Durban.
- Schuldt, A., Baruffol, M., Bohnke, M., Bruelheide, H., Hardtle, W., Lang, A. C., Nadrowski, K., von Oheimb, G., Voigt, W., Zhou, H. Z., and Assmann, T. (2010). Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98, 917–926.
- Schuldt, A., Both, S., Bruelheide, H., Hardtle, W., Schmid, B., Zhou, H. Z., and Assmann, T. (2011). Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *Plos One* 6, e22905.
- Sekercioglu, C. H., Loarie, S. R., Brenes, F. O., Ehrlich, P. R., and Daily, G. C. (2007). Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology* 21, 482–494.
- Sizer, N. and Tanner, E. V. J. (1999). Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* 91, 135–142.
- Smithers, H. N. (2000). *Smithers' mammals of southern Africa - a field guide*. Struik Publishers, Cape Town.
- Sobek, S., Scherber, C., Steffan-Dewenter, I., and Tschamntke, T. (2009). Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160, 279–288.

- Sork, V. L. (1987). Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68, 1341–1350.
- Steffan-Dewenter, I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* 17, 1036–1044.
- Stenseth, N. C., Leirs, H., Skonhøft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Singleton, G. R., Lima, M., Machang'u, R. S., Makundi, R. H., Zhang, Z. B., Brown, P. R., Shi, D. Z., and Wan, X. R. (2003). Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* 1, 367–375.
- Stoner, K. E., Riba-Hernandez, P., Vulinec, K., and Lambert, J. E. (2007). The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica* 39, 316–327.
- Stuart, C. T. and Stuart, M. D. (2007). Field guide to mammals of southern Africa. Struik Publishers, Cape Town.
- Tabarelli, M., Da Silva, M. J. C., and Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation* 13, 1419–1425.
- Tahvanai, J. O. and Root, R. B. (1972). Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10, 321–346.
- Takele, S., Bekele, A., Belay, G., and Balakrishnan, M. (2011). A comparison of rodent and insectivore communities between sugarcane plantation and natural habitat in Ethiopia. *Tropical Ecology* 52, 61–68.
- Tallmon, D. A., Jules, E. S., Radke, N. J., and Mills, L. S. (2003). Of mice and men and *Trillium*: cascading effects of forest fragmentation. *Ecological Applications* 13, 1193–1203.

- Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D., and Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science* 294, 1923–1926.
- Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., and Paine, C. E. T. (2008). Tree recruitment in an empty forest. *Ecology* 89, 1757–1768.
- Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I., and Townsend, P. (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 99, 12923–12926.
- Tofoli, C. F., Rohe, F., and Setz, E. Z. F. (2009). Jaguarundi (*Puma yagouaroundi*) (Geoffroy, 1803) (Carnivora, Felidae) food habits in a mosaic of Atlantic rainforest and eucalypt plantations of southeastern Brazil. *Brazilian Journal of Biology* 69, 873–877.
- Tscharntke, T., Klein, A. M., Krüss, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters* 8, 857–874.
- Tsvuura, Z., Griffiths, M. E., and Lawes, M. J. (2007). The effect of herbaceous understory cover on fruit removal and seedling survival in coastal dune forest trees in South Africa. *Biotropica* 39, 428–432.
- Turner, I. M. and Corlett, R. T. (1996). The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution* 11, 330–333.
- Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351–1363.
- Umetsu, F., Naxara, L., and Pardini, R. (2006). Evaluating the efficiency of pitfall traps for sampling small mammals in the neotropics. *Journal of Mammalogy* 87, 757–765.

- Umetsu, F. and Pardini, R. (2007). Small mammals in a mosaic of forest remnants and anthropogenic habitats-evaluating matrix quality in an Atlantic forest landscape. *Landscape Ecology* 22, 517–530.
- Unsicker, S. B., Baer, N., Kahmen, A., Wagner, M., Buchmann, N., and Weisser, W. W. (2006). Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. *Oecologia* 150, 233–246.
- Unsicker, S. B., Oswald, A., Kohler, G., and Weisser, W. W. (2008). Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia* 156, 313–324.
- van Wyk, B. and van Wyk, P. (2007). Field guide to trees of southern Africa. Struik Publishers, Cape Town.
- Vandermeer, J. and Perfecto, I. (2007). The agricultural matrix and a future paradigm for conservation. *Conservation Biology* 21, 274–277.
- Vehviläinen, H., Koricheva, J., and Ruohomäki, K. (2007). Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. *Oecologia* 152, 287–298.
- von Maltitz, G., Mucina, L., Geldenhuys, C. J., Lawes, M. J., Eeley, H., Aidié, H., Vink, D., Fleming, G., and Bailey, C. (2003) Classification system for South African indigenous forests: An objective classification for the Department of Water Affairs and Forestry. ENV-P-C 2003-017, 275. CSIR, Pretoria.
- Wang, B. C. and Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution* 17, 379–385.
- Wenny, D. G. (2000). Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70, 331–351.

- White, J. A. and Whitham, T. G. (2000). Associational susceptibility of cottonwood to a Box Elder herbivore. *Ecology* 81, 1795–1803.
- Wilson, J. W., Stirnemann, R. L., Shaikh, Z. S., and Scantlebury, M. (2010). The response of small mammals to natural and human-altered edges associated with Afromontane forests of South Africa. *Forest Ecology and Management* 259, 926–931.
- Wirminghaus, J. O. and Perrin, M. R. (1992). Diets of small mammals in a southern African temperate forest. *Israel Journal of Zoology* 38, 353–361.
- Wirminghaus, J. O. and Perrin, M. R. (1993). Seasonal changes in density, demography and body-composition of small mammals in a southern temperate forest. *Journal of Zoology* 229, 303–318.
- Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., and Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science* 321, 123–126.
- Wright, S. J. and Duber, H. C. (2001). Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.
- Wright, S. J. and Muller-Landau, H. C. (2006). The future of tropical forest species. *Biotropica* 38, 287–301.

9 Appendix

Appendix chapter 2

Appendix 1. Number of rodents per species, percentage of ground vegetation cover and seed predation per plot and study site in large natural forest fragments with forest matrix (ForFra) and in small forest fragments surrounded by natural grassland (GraFra), plantations (PlaFra) and agriculture (AgrFra). VC = Vernon Crookes nature reserve; OG = Oribi Gorge nature reserve; NA = not applicable.

Forest fragment type (trap nights) Study site	Plot	<i>Dendromus mesomelas</i>	<i>Dendromus mystacalis</i>	<i>Grammomys dolichurus</i>	<i>Lemniscomys rosalia</i>	<i>Mastomys</i> sp.	<i>Mus minutoides</i>	<i>Rhabdomys pumilio</i>	Ground vegetation (%)	Seed predation (%)
ForFra (360)	VC 1	-	-	-	-	-	-	-	10	27.3
	VC 2	-	-	-	-	-	-	-	20	27.3
	OG 3	-	-	-	-	-	-	-	0	6.7
	OG 4	-	-	-	-	-	-	-	0	18.7
	OG 5	-	-	-	-	-	-	-	10	18.7
	OG 6	-	-	-	-	-	-	-	0	12.7
GraFra (300)	VC 1	NA	NA	NA	NA	NA	NA	NA	60	14.7
	VC 2	-	-	-	-	-	-	-	0	22.7
	VC 3	-	-	-	-	-	-	-	0	22.0
	VC 4	-	-	-	-	1	2	-	35	54.7
	VC 5	-	-	-	-	-	-	-	0	35.3
	VC 6	-	1	-	-	-	-	-	50	5.3
PlaFra (360)	VC 1	-	-	-	-	-	-	-	50	7.3
	VC 2	-	-	-	-	-	-	-	20	45.3
	VC 3	-	-	-	-	-	-	-	40	10.7
	VC 4	-	1	1	-	-	-	-	70	31.3
	VC 5	-	-	-	-	-	-	-	75	10.7
	VC 6	-	-	-	-	-	-	2	75	1.3
AgrFra (360)	VC 1	1	-	-	-	3	-	-	55	48.0
	VC 2	-	-	-	-	-	-	-	65	58.7
	VC 3	-	-	-	-	9	-	-	85	51.3
	VC 4	-	-	-	-	-	-	-	60	NA
	VC 5	-	-	-	-	-	-	1	60	34.7
	OG 6	-	-	-	2	1	-	-	50	28.7

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Appendix 2. Successional status (Suc: ES = early-, LS = late-successional), dispersal mode (DM: G = gravity, W = wind, Z = zoochorous) and presence (+) or absence (-) of tree (Tr), seedling (Se) and sapling (Sa) species in large natural forest fragments with forest matrix (ForFra) and in small forest fragments surrounded by natural grassland (GraFra), plantations (PlaFra) and agriculture (AgrFra).

Species (family)	Suc	DM	ForFra			GraFra			PlaFra			AgrFra		
			Tr	Se	Sa	Tr	Se	Sa	Tr	Se	Sa	Tr	Se	Sa
<i>Acacia caffra</i> (Thunb.) Willd. (Fabaceae)	LS	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Acacia mearnsii</i> De Wild. (Fabaceae)	ES	Z	-	-	-	-	-	-	-	+	+	-	-	-
<i>Acalypha glabrata</i> Thunb. var. <i>glabrata</i> (Euphorbiaceae)	ES	Z	+	+	+	-	-	+	-	-	-	+	-	-
<i>Acokanthera oppositifolia</i> (Lam.) Codd (Apocynaceae)	LS	Z	-	-	+	-	-	-	-	-	-	+	-	+
<i>Acridocarpus natalitius</i> A.Juss. var. <i>natalitius</i> (Malpighiaceae)	LS	W	-	-	+	-	-	-	-	-	-	-	-	-
<i>Albizia adianthifolia</i> (Schumach.) W.Wight var. <i>adianthifolia</i> (Fabaceae)	ES	Z	+	-	-	-	-	-	-	-	-	+	-	+
<i>Allophylus africanus</i> P.Beauv. var. <i>africanus</i> (Sapindaceae)	ES	Z	+	-	-	-	+	-	-	+	-	+	-	+
<i>Allophylus dregeanus</i> (Sond.) De Winter (Sapindaceae)	ES	Z	-	-	-	+	+	+	+	+	-	+	-	-
<i>Antidesma venosum</i> E.Mey. ex Tul. (Euphorbiaceae)	ES	Z	+	-	-	-	-	-	-	-	-	+	-	-
<i>Apodytes dimidiata</i> E.Mey. ex Arn. subsp. <i>dimidiata</i> (Icacinaceae)	ES	Z	-	-	-	+	+	-	+	-	-	+	+	+
<i>Bachmannia woodii</i> (Oliv.) Gilg (Capparaceae)	LS	Z	-	-	+	-	-	-	-	-	-	-	-	-
<i>Baphia racemosa</i> (Hochst.) Baker (Fabaceae)	LS	G	+	+	+	-	-	-	-	-	-	-	-	-
<i>Bersama swinnyi</i> E.Phillips (Melianthaceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Bersama tysoniana</i> Oliv. (Melianthaceae)	LS	Z	+	-	-	+	-	+	-	-	-	+	+	-
<i>Brachylaena discolor</i> DC. (Asteraceae)	LS	W	-	-	-	+	-	-	-	-	-	+	-	-

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<i>Brachylaena elliptica</i> (Thunb.) DC. (Asteraceae)	LS	W	+	-	-	-	-	-	-	-	-	-	-	-
<i>Brachylaena uniflora</i> Harv. (Asteraceae)	LS	W	+	-	-	-	-	-	-	-	-	-	-	-
<i>Bridelia micrantha</i> (Hochst.) Baill. (Euphorbiaceae)	LS	Z	+	-	-	+	-	-	-	-	-	+	-	-
<i>Burchellia bubalina</i> (L.f.) Sim (Rubiaceae)	LS	Z	-	-	-	-	-	-	-	-	-	-	-	+
<i>Calodendrum capense</i> (L.f.) Thunb. (Rutaceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Calpurnia aurea</i> (Aiton) Benth. subsp. <i>aurea</i> (Fabaceae)	ES	Z	-	-	-	-	+	-	-	-	-	-	-	-
<i>Canthium ciliatum</i> (Klotzsch ex Eckl. & Zeyh) Kuntze (Rubiaceae)	LS	Z	-	-	-	+	+	+	-	+	+	+	+	+
<i>Canthium inerme</i> (L.f.) Kuntze (Rubiaceae)	LS	Z	+	-	-	-	+	-	-	-	-	+	-	+
<i>Canthium spinosum</i> (Klotzsch ex Eckl. & Zeyh) Kuntze (Rubiaceae)	ES	Z	+	-	-	+	-	+	+	-	+	+	-	+
<i>Canthium suberosum</i> Codd (Rubiaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Carissa macrocarpa</i> (Eckl.) A.DC. (Apocynaceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Cassine peragua</i> L. subsp. <i>peragua</i> (Celastraceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Cassipourea gummiflua</i> Tul. var. <i>Verticillata</i> (Rhizophoraceae)	LS	Z	+	+	-	+	+	+	-	-	-	-	-	-
<i>Cassipourea malosana</i> (Baker) Alston (Rhizophoraceae)	LS	Z	+	-	+	+	+	+	-	-	-	+	-	-
<i>Caturanegam obovata</i> (Hochst.) A.E.Gonç. (Rubiaceae)	ES	Z	-	-	-	+	+	+	-	-	-	-	-	-
<i>Celtis africana</i> Burm.f. (Celtidaceae)	ES	Z	+	+	-	+	+	+	+	+	+	+	-	-
<i>Cestrum laevigatum</i> Schltr. (Solanaceae)	ES	Z	-	-	-	-	-	-	+	+	+	-	-	-
<i>Chaetachme aristata</i> Planch. (Celtidaceae)	LS	Z	+	-	-	+	+	-	-	-	-	-	-	-
<i>Clausena anisata</i> (Willd.) Hook.f. ex Benth. (Rutaceae)	ES	Z	+	+	-	-	-	-	-	-	-	+	-	+
<i>Clerodendrum glabrum</i> E.Mey. var. <i>glabrum</i> (Lamiaceae)	ES	Z	+	-	-	+	-	-	+	-	+	+	-	-

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<i>Cnestis polyphylla</i> Lam. (Connaraceae)	LS	Z	-	-	-	-	-	-	-	+	+	-	-	+
<i>Combretum erythrophyllum</i> (Burch.) Sond. (Combretaceae)	ES	Z	+	-	-	+	+	-	+	+	+	+	+	+
<i>Combretum kraussii</i> Hochst. (Combretaceae)	LS	W	+	+	+	+	+	+	+	+	+	+	+	+
<i>Commiphora harveyi</i> (Engl.) Engl. (Burseraceae)	LS	W	-	-	-	-	-	-	-	-	-	-	-	-
<i>Commiphora woodii</i> Engl. (Burseraceae)	LS	Z	-	-	-	-	+	-	-	-	-	-	-	-
<i>Croton sylvaticus</i> Hochst. ex C.Krauss (Euphorbiaceae)	ES	Z	+	-	-	+	-	-	+	-	-	+	-	-
<i>Cryptocaria myrtifolia</i> Stapf (Lauraceae)	LS	Z	-	-	-	-	-	+	-	-	-	-	-	-
<i>Cryptocaria woodii</i> Engl. (Lauraceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Cryptocaria wyliei</i> Stapf (Lauraceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Cunonia capensis</i> L. (Cunoniaceae)	ES	Z	-	-	-	+	-	-	-	-	-	+	-	-
<i>Cussonia sphaerocephala</i> Strey (Araliaceae)	LS	Z	+	-	-	+	-	-	-	-	-	+	-	-
<i>Cussonia spicata</i> Thunb. (Araliaceae)	ES	Z	+	-	-	-	-	-	-	-	-	+	-	-
<i>Deinbollia oblongifolia</i> (E.Mey. ex Arn.) Radlk. (Sapindaceae)	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Diospyros lycioides</i> Desf. subsp. <i>sericea</i> (Ebenaceae)	ES	Z	+	+	+	-	-	+	+	-	+	+	-	-
<i>Diospyros villosa</i> (L.) De Winter var. <i>villosa</i> (Ebenaceae)	ES	Z	-	-	-	-	-	-	+	-	-	-	-	-
<i>Dombeya burgessiae</i> Gerrard ex Harv. (Sterculiaceae)	ES	G	+	-	-	-	-	-	-	-	-	+	-	-
<i>Dombeya tiliaceae</i> (Endl.) Planch. (Sterculiaceae)	ES	G	-	-	-	-	-	-	-	-	+	-	-	-
<i>Dovyalis lucida</i> Sim (Flacourtiaceae)	ES	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Dovyalis rhamnoides</i> (Burch. ex DC.) Burch. & Harv. (Flacourtiaceae)	ES	Z	-	-	-	-	-	-	+	+	+	+	-	-
<i>Dracaena aletiformis</i> (Haw.) Bos (Dracaenaceae)	ES	Z	+	-	-	+	-	-	+	+	+	+	-	+

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<i>Drypetes arguta</i> (Müll.Arg.) Hutch. (Euphorbiaceae)	LS	Z	+	+	+	-	-	+	-	-	-	-	-	+
<i>Drypetes gerrardii</i> Hutch. var. <i>gerrardii</i> (Euphorbiaceae)	LS	Z	+	+	-	+	-	+	+	-	-	+	+	+
<i>Ekebergia capensis</i> Sparrm. (Meliaceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Elaeodendron croceum</i> (Thunb.) DC. (Celastraceae)	ES	Z	+	+	+	+	-	-	-	-	-	+	-	+
<i>Englerophytum natalense</i> (Sond.) T.D.Penn (Sapotaceae)	LS	Z	+	+	+	+	+	+	-	-	-	+	-	-
<i>Erythrina caffra</i> Thunb. (Fabaceae)	ES	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Erythrina lysistemon</i> Hutch. (Fabaceae)	ES	Z	-	-	-	-	-	-	-	-	+	-	-	-
<i>Erythrococca</i> sp. nov. (Euphorbiaceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Eucalyptus grandis</i> W.Hill ex Maiden (Myrtaceae)	ES	G	-	-	-	-	-	-	+	-	-	-	-	-
<i>Euclea natalensis</i> A.DC. subsp. <i>natalensis</i> (Ebenaceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Eugenia natalitia</i> Sond. (Myrtaceae)	LS	Z	-	-	-	+	+	+	+	-	+	+	-	+
<i>Eugenia umtamvounensis</i> A.E.von Wyk (Myrtaceae)	LS	Z	+	+	+	-	-	-	-	+	-	-	-	-
<i>Eugenia woodii</i> Dummer (Myrtaceae)	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Faurea saligna</i> Harv. (Proteaceae)	ES	W	-	-	-	-	-	-	-	-	+	-	-	-
<i>Ficus burkei</i> (Miq.) Miq. (Moraceae)	ES	Z	+	-	-	+	-	-	-	-	-	-	-	-
<i>Ficus burtt-davyi</i> Hutch. (Moraceae)	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Ficus craterostoma</i> Warb. ex Mildbr. & Burret (Moraceae)	LS	Z	-	-	-	+	-	-	+	-	-	+	-	-
<i>Ficus natalensis</i> Hochst. subsp. <i>natalensis</i> (Moraceae)	ES	Z	+	-	-	-	-	-	-	-	-	+	-	-
<i>Ficus sur</i> Forssk. (Moraceae)	ES	Z	-	-	-	+	-	-	+	-	-	+	-	-
<i>Gardenia thunbergia</i> L.f. (Rubiaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Grewia lasiocarpa</i> E.Mey. ex Harv. (Tiliaceae)	LS	Z	-	-	-	+	+	+	+	+	+	+	-	+
<i>Grewia occidentalis</i> L. var.	ES	Z	-	-	-	+	-	-	+	-	-	+	-	-

<i>occidentalis</i> (Tiliaceae)														
<i>Gymnosporia buxifolia</i> (L.) Szyszyl. (Celastraceae)	ES	Z	-	-	-	-	-	+	-	-	-	+	-	-
<i>Gymnosporia harveyana</i> Loes. (Celastraceae)	LS	Z	+	-	-	-	+	+	-	-	-	+	+	+
<i>Gymnosporia nemorosa</i> (Eckl. & Zeyh.) Szyszyl. (Celastraceae)	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Halleria lucida</i> L. (Scrophulariaceae)	ES	Z	-	-	-	-	-	-	+	-	+	+	-	+
<i>Harpephyllum caffrum</i> Bernh. ex C.Krauss (Anarcardiaceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Heywoodia lucens</i> Sim (Euphorbiaceae)	ES	G	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hippobromus pauciflorus</i> (L.f.) Radlk. (Sapindaceae)	ES	Z	-	-	-	-	+	-	-	-	-	-	-	-
<i>Hyperacanthus amoenus</i> (Sims) Bridson (Rubiaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Kiggelaria africana</i> L. (Flacourtiaceae)	ES	Z	-	-	-	-	-	-	+	-	+	-	-	-
<i>Macaranga capensis</i> (Baill.) Benth. ex Sim (Euphorbiaceae)	ES	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Maerua cafra</i> (DC.) Pax (Capparaceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Maesa lanceolata</i> Forssk. (Maesaceae)	ES	Z	+	-	-	-	-	-	+	+	+	+	-	+
<i>Margaritaria discoidea</i> (Baill.) G.L.Webster var. <i>fagifolia</i> (Pax) Radcl.-Sm. (Euphorbiaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Maytenus abbottii</i> A.E.von Wyk (Celestraceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Maytenus acuminata</i> (L.f.) Loes. (Celestraceae)	ES	Z	-	-	-	-	-	-	-	+	-	-	-	-
<i>Maytenus peduncularis</i> (Sond.) Loes. (Celastraceae)	LS	Z	-	-	-	-	-	-	-	-	-	+	-	-
<i>Maytenus undata</i> (Thunb.) Blakelock (Celastraceae)	ES	Z	-	-	-	-	-	-	+	-	-	-	-	-
<i>Memecylon natalense</i> Markgr. (Melastomataceae)	LS	Z	-	+	-	+	-	-	-	-	-	-	-	-
<i>Millettia grandis</i> (E.Mey.) Skeels (Fabaceae)	ES	G	+	+	+	+	-	-	-	-	-	-	-	-

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<i>Mimusops obovata</i> Sond. (Sapotaceae)	LS	Z	+	-	-	-	-	-	-	-	-	+	-	-
<i>Nectaropetalum capense</i> (Bolus) Stapf & Boodle (Erythroxylaceae)	LS	Z	+	-	+	-	-	-	-	-	-	-	-	-
<i>Obetia tenax</i> (N.E.Br.) Friis (Urticaceae)	ES	G	+	-	+	-	-	-	-	-	-	+	-	-
<i>Ochna arborea</i> Burch. ex DC. var. <i>arborea</i> (Ochnaceae)	LS	Z	+	+	+	-	+	-	-	-	-	-	-	-
<i>Ochna serrulata</i> (Hochst.) Walp. (Ochnaceae)	ES	Z	-	-	+	-	+	+	-	+	-	-	+	-
<i>Olea capensis</i> L. subsp. <i>macrocarpa</i> (C.H.Wright) I.Verd. (Oleaceae)	LS	Z	-	-	+	-	-	-	-	-	-	-	-	-
<i>Oricia bachmannii</i> (Engl.) I.Verd. (Rutaceae)	LS	Z	+	-	+	-	-	-	-	-	-	-	-	-
<i>Pavetta bowkeri</i> Harv. (Rubiaceae)	LS	Z	-	-	-	-	-	-	-	+	-	-	-	+
<i>Pavetta lanceolata</i> Eckl. (Rubiaceae)	ES	Z	-	-	-	-	-	-	+	+	+	+	-	-
<i>Peddiea africana</i> Harv. (Thymelaeaceae)	LS	Z	+	+	-	+	+	+	+	+	+	-	+	+
<i>Phoenix reclinata</i> Jacq. (Arecaceae)	ES	Z	+	+	+	+	+	+	-	+	+	-	-	-
<i>Pittosporum viridiflorum</i> Sims (Pittosporaceae)	ES	Z	+	-	-	+	-	-	-	-	-	+	-	+
<i>Pleurostyliia capensis</i> (Turcz.) Loes. (Celastraceae)	LS	Z	+	-	+	+	+	+	+	-	-	+	-	+
<i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb. (Anacardiaceae)	LS	Z	-	-	-	-	-	-	-	+	+	-	-	-
<i>Protorhus longifolia</i> (Bernh.) Engl. (Celastraceae)	ES	Z	+	+	-	+	+	+	+	+	+	+	+	
<i>Pseudosclopia polyantha</i> Gilg (Flacourtiaceae)	ES	G	-	-	-	-	-	-	-	-	+	-	-	-
<i>Psychotria capensis</i> (Eckl.) Vatke subsp. <i>capensis</i> var. <i>Capensis</i> (Rubiaceae)	ES	Z	+	-	+	+	+	+	+	+	+	+	+	+
<i>Rapanea melanophloeos</i> (L.) Mez (Myrsinaceae)	ES	Z	+	-	+	+	+	+	-	-	-	+	+	+
<i>Rauvolfia caffra</i> Sond. (Apocynaceae)	ES	Z	+	+	-	-	+	-	-	-	-	-	-	-
<i>Rawsonia lucida</i> Harv. & Sond. (Flacourtiaceae)	LS	G	-	-	-	+	+	+	-	-	-	-	-	-

Appendix chapters 3 and 4

<i>Searsia chiridensis</i> (Baker f.) Moffett (Anacardiaceae)	ES	Z	+	-	-	+	-	+	+	-	-	+	-	+
<i>Searsia dentata</i> Thunb. (Anacardiaceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Rothmannia globosa</i> (Hochst.) Keay (Rubiaceae)	LS	Z	+	-	-	-	+	-	-	-	-	+	+	+
<i>Schrebera alata</i> (Hochst.) Welw. (Oleaceae)	ES	W	+	-	-	-	-	-	-	-	-	-	-	-
<i>Scolopia zeyheri</i> (Nees) Harv. (Flacourtiaceae)	ES	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Strelitzia nicolai</i> Regel & Körn. (Strelitziaceae)	ES	Z	+	-	+	+	+	+	+	-	+	-	-	-
<i>Strychnos decussata</i> (Pappe) Gilg (Strychnaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Strychnos henningsii</i> Gilg (Strychnaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Strychnos usambarensis</i> Gilg (Strychnaceae)	LS	Z	+	+	+	-	-	-	-	-	-	-	-	-
<i>Syzygium cordatum</i> Hochst. ex C.Krauss (Myrtaceae)	ES	Z	+	-	-	+	-	-	+	-	+	+	-	-
<i>Vangueria parviflora</i> Sond. (Rubiaceae)	ES	Z	-	-	-	-	-	-	-	-	+	-	-	-
<i>Tarenna pavettoides</i> (Harv.) Sim subsp. <i>pavettoides</i> (Rubiaceae)	ES	Z	+	+	-	-	-	-	-	-	-	-	-	-
<i>Teclea gerrardii</i> I.Verd. (Rutaceae)	LS	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Teclea natalensis</i> (Sond.) Engl. (Rutaceae)	LS	Z	+	+	-	+	-	-	-	-	-	-	-	-
<i>Trema orientalis</i> (L.) Blume (Celtidaceae)	ES	Z	-	-	-	+	-	-	+	+	-	+	-	-
<i>Tricalysia capensis</i> (Meisn. ex Hochst) var. <i>capensis</i> (Rubiaceae)	ES	Z	-	-	-	-	-	-	-	-	-	+	-	+
<i>Tricalysia sonderiana</i> Hiern (Rubiaceae)	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-
<i>Trichilia dregeana</i> Sond. (Meliaceae)	ES	Z	-	-	-	+	-	-	-	-	-	-	-	-
<i>Vangueria infausta</i> Burch. (Rubiaceae)	ES	Z	-	-	-	-	+	-	-	-	+	+	-	-
<i>Vepris lanceolata</i> (Lam.) G.Don. (Rutaceae)	ES	Z	-	-	-	+	-	+	+	-	-	+	+	+
<i>Xylothea kraussiana</i> Hochst.	ES	Z	+	-	-	-	-	-	-	-	-	-	-	-

9 – Appendix

(Flacourtiaceae)

Xymalos monospora (Harv.) LS Z - - - + + - - - - - -

Baill (Monimiaceae)

Zanthoxylum capense (Thunb.) ES Z - - - + + - + - + + - -

Harv. (Rutaceae)

Zanthoxylum davyi (I.Verd.) LS Z - - - + - - - - - - - +

P.G.Waterman (Rutaceae)

Danksagung

Danksagung

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Die Seiten 115-116 (restliche Danksagung) enthalten persönliche Informationen. Sie sind deshalb weder Bestandteil der Universitätsbibliotheks-Exemplare, noch der Online-Veröffentlichung.—*Pages 115–116 contain personal information and are therefore neither included in the printed versions for the library nor in the online version of this dissertation.*

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Erklärung

Hiermit versichere, dass ich meine Dissertation mit dem Titel

‘Fragment quality rather than matrix habitat shapes forest regeneration in a South African mosaic-forest landscape’

selbständig und ohne unerlaubte Hilfe angefertigt habe und mich keiner als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Diese Dissertation wurde außerdem in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg an der Lahn, April 2012

Alexandra Botzat