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S04-4 The role of birds in seed dispersal and its consequences for forest ecosystems

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Abstract In tropical forests, most trees have fleshy fruits adapted to animal dispersal; and the important role that birds especially play in their dispersal is well documented. Few studies, however, have so far addressed the question of whether declining bird species richness, whatever the cause, leads to changes, even breakdown, in seed dispersal and plant regeneration processes. In this paper we present a comparative approach to this question by comparing seed dispersal in two closely related tree species of the genus *Commiphora* (family Burseraceae) in two areas with disparate richness in avian frugivores: South Africa and Madagascar. In South Africa, where frugivore diversity is high, relatively high numbers of bird species (12) dispersed seeds leading to high dispersal percentages (70.8%). Consequently, seedlings established away from parent trees, producing an evenly dispersed distribution in the adult tree population. But in Madagascar, which is strikingly depauperate in avian frugivores, few bird species (3) dispersed seeds, leading to very low dispersal percentages (7.9%). Consequently, seedlings established close to and under parent trees, resulting in a clumped distribution of adult trees. Secondary dispersal by ants was also markedly different between the two sites, with high dispersal (47.9%) in Madagascar and no dispersal in South Africa. These results indicate that bird species richness influences seed dispersal and seedling establishment, and thus might have far-reaching consequences for the floristic composition and structure of ecosystems. Furthermore, our studies show the need for broad ecological approaches into the vectors of seed dispersal, as other processes, e.g., secondary dispersal, might also be important for forest regeneration.

Key words Bird dispersal, Bird species richness, Mutualistic plant-animal-interactions, Regeneration, Seedling establishment

1 Introduction

The most famous and frequently cited example of mutualistic interaction between a frugivorous bird and its fruit plant is that of the dodo (*Raphus cucullatus*) and the calvaria tree (*Sideroxylon majus*). The dodo, once native to Mauritius but extinct by 1681, was said to play an integral role in the dispersal of calvaria seeds. Temple (1977) even went so far as to suggest an obligate mutualism between dodo and tree, thereby explaining the failure of the tree to regenerate by the dodo's extinction. This example of obligate mutualism has appealed to many ecologists and has long become textbook dogma exemplifying tight ecological interdependence among species. Yet there is little evidence that obligate mutualisms in seed dispersal really exist. Although more than 90% of all tree and shrub species in tropical forests develop fleshy fruits adapted to animal dispersal (Howe and Smallwood, 1982), interactions between seed dispersers and plants are in general less tight than, for example, those between pollinators and plants. Rather, they are rather diffuse and nonspecific: seeds of a given plant species are commonly dispersed by a variety of animals (Coates-Estrada and Estrada, 1988; Fleming and Williams, 1990). With such diffuse interactions, the question arises whether seed dispersers have the potential to exert influence on their interactive partners, the plants themselves.

Many studies indicate that worldwide habitat loss and fragmentation lead to a decline in bird species richness (see review in Turner, 1996; Brooks et al., 1999). It is also known that dispersal mutualists such as birds are important for seed dispersal, for without them seedling recruitment is limited due to the high mortality in non-dispersed seeds that merely fall beneath parent trees (Janzen et al., 1976; Augspurger, 1983; Howe et al., 1985). However, understanding of the link between bird species richness and its consequences for forest regeneration is still meagre. Few studies have addressed the consequences of disperser declines for plant populations, although some possible scenarios have been presented (e.g., Howe, 1984; Bond, 1995). Pizo (1997) found that local bird species richness determined the frugivore assemblages of fruiting trees, with a higher number of more reliable and efficient bird species visiting trees and dispersing seeds in a large forest site than in a small forest fragment. Santos and Telleria (1994) also showed in a comparison of large and small forest sites that a low number of dispersal agents at the small sites, both in species and abundance, led to a reduction in seed transfer and seedling

establishment in *Juniper* trees.

At the community level, Cordeiro and Howe (2001) found a decline in frugivorous birds and primates with decreasing site-fragment size in the Eastern Usambara Mountains in Tanzania. When relating this to seedling recruitment, the density of regeneration in 31 animal-dispersed tree species was found to increase with patch size, with highest numbers in large and lowest numbers in small fragments. In contrast, recruitment of wind- and gravity-dispersed trees was unaffected.

We conducted comparative studies in South Africa (high frugivore richness) and Madagascar (low frugivore richness) to investigate whether frugivore richness influences the seed dispersal system of tree species and whether this has consequences for seedling establishment and the spatial distribution of seedlings and trees (also Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). For this we screened the seed dispersal system of two related tree species: *Commiphora harveyi* in Oribi Gorge Nature Reserve, Natal, South Africa, and *C. guillaumini* in Kirindy Forest on the west coast of Madagascar. Both have similar, bird-dispersed fruits.

2 Results

2.1 Seed dispersal by birds

Corresponding to high bird diversity in South Africa, 15 frugivore species visited *Commiphora* trees at the South African site, 12 of them contributing to seed dispersal (Table 1; Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). In Madagascar, with low avian diversity, only 6 frugivores visited the trees at our site there (Table 1, Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). Only 3 Malagasy frugivores dispersed *Commiphora* seeds, the primary contributor (lesser vasa parrot, *Coracopsis nigra*) moreover being a seed waster which dropped most of the seeds to the ground. As a result of these disparities, we found that 70.8 % of all seeds were dispersed per tree in South Africa but only 7.9 % in Madagascar (Table 1; Bleher and Böhning-Gaese, 2001).

2.2 Secondary seed dispersal by ants

Commiphora seeds at the Malagasy study site were dispersed secondarily by ants (47.9% of all seeds). However, seeds were not carried any great distance, and their dispersal contributed little to seedling establishment in comparison with those dispersed by birds (Böhning-Gaese et al., 1999; Böhning-Gaese and Bleher, 2000). At the South African site, in contrast, there was no seed dispersal by ants (Voigt et al., 2002). Poor ant dispersal in South Africa is due to a lack of potential dispersers, low ant activity and few aggressive interspecific interactions among ant species (Voigt et al., 2002).

2.3 Seedling establishment

The differences in bird species numbers and dispersal percentages between the two sites translated to differences in seedling distribution and survival. At the South African site, where most seeds were dispersed, seedlings were found mostly away from parent trees: median distance 21.1 m. At the Malagasy site, however, where most seeds fell under parent trees, most seedlings were found there: median distance 0.9 m (Bleher and Böhning-Gaese, 2001). Moreover, although seedling establishment per hectare was much the same at both sites, survival probability for first-year seedlings differed. In South Africa, 36% of all seedlings survived the first year compared to only 15% in Madagascar (Bleher and Böhning-Gaese, 2001).

2.4 Tree distribution

Our field data using the T-Square-method indicate a

Table 1 Primary seed dispersal by birds, secondary dispersal by ants, seedling distribution, survival probability of first year-seedlings, and distribution of adult trees of the genus *Commiphora* at two study sites in South Africa and Madagascar

	South Africa	Madagascar
Primary dispersal by birds		
Bird frugivore richness	high (14)	low (4)
Bird species visiting trees	15	6
Bird species dispersing seeds	12	3
Percentage of seeds dispersed per tree	70.8%	7.9%
Secondary dispersal by ants		
Potential ant dispersers (assumed from seed size)	absent	present
Ant activity	low	high
Percentage of seeds secondarily dispersed per tree	0%	47.9%
Seedling establishment and tree distribution		
Seedling distribution	away from parent	under parent
Seedling survival	high (36%)	low (15%)
Tree distribution	uniform	clumped

Data from Böhning-Gaese et al., 1999; Böhning-Gaese and Bleher, 2000; Bleher and Böhning-Gaese, 2001; Bleher et al., 2002; Voigt et al., 2002.

rather uniform distribution of the tree populations at the South African study site in contrast to a clumped distribution at the Malagasy site (Bleher and Böhning-Gaese, 2001). A computer simulation model evaluating the influence of different factors such as dispersal distance, tree density, breeding system and seedling distribution on the spatial distribution of tree populations confirmed the importance of dispersal distance. This, in turn, can be traced back to the presence/absence of animal dispersers (Bleher et al., 2002).

3 Discussion

Animal-plant mutualisms are usually not as tight as suggested by the example of the dodo and the calvaria tree. However, the results of our comparative studies in South Africa and Madagascar indicate that bird species richness does affect seed dispersal, which has carry-on effects on plant life cycles (Bleher and Böhning-Gaese, 2001). Therefore, bird dispersers have a potential influence on their interactive partners, even though the extinction of frugivorous birds might not lead to immediate extinction cycles in plant communities as predicted by various scenarios (Howe, 1984; Bond, 1995)

Although bird diversity is of concern worldwide, very few studies have examined quantitatively the effect of bird species richness on seed dispersal and regeneration of plant populations. The scarcity of relevant studies lies in difficulties in approach: an experimental approach has to be excluded from an ethical point of view; and comparative approaches using continuous forest and forest fragments often face the problem of finding adequate sample sizes as well as standardized sites, i.e., fragments not influenced by complicating factors. Therefore, our cross-continent approach of comparing sites or continents with disparate species richness might be a useful alternative.

The island of Madagascar is depauperate in frugivorous birds in comparison with other tropical areas, and lemurs appear to play a prominent role in seed dispersal instead (Scharfe and Schlund, 1996; Goodman et al., 1997; Dew and Wright, 1998). Historical extinction does not appear to be the reason for the poor frugivorous avifauna in Madagascar (Langrand, 1990; Goodman and Rakotozafy, 1997). Rather, it may be linked to reduced diversity in species of *Ficus* (Goodman and Ganzhorn, 1997), which are a keystone resource for frugivores in most tropical forests (e. g., Terborgh, 1986; Bleher et al., 2003).

Although birds seem to play a crucial role in the dispersal of plants, with consequences for forest ecosystems such as shown in our studies, other factors and processes have to be taken into consideration as well. Such factors are abiotic (e.g., light, moisture) as well as biotic (e.g., secondary dispersal, seed predation). Secondary dispersers, for example, can alter the pattern of seed dispersal as shown by one of our studies (Böhning-Gaese et al., 1999). Comparative studies across sites and anthropogenic deconstruction experiments, based on broader perspective of plant-animal-interactions, might "close the dispersal loop" (Wang and Smith, 2002) and give us a better understanding of the long-term consequences of animal species richness for plant populations.

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