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Seed dispersal and predation across a grassland-forest ecotone in southern Palawan, Philippines

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Introduction

Southeast Asia belongs to the world's regions with the highest rates of forest loss, with about 2.3 million ha, or roughly one percent of the total forest cover being destroyed annually (Appanah, 2003). In large areas, removal of the original tree cover, predominantly through logging, unsustainable forms of agriculture, livestock grazing or recurrent fires have resulted in the formation of permanent grass-dominated vegetation types (FAO, 2003). The Philippines are severely affected in particular, mostly because, in contrast to other countries in the region, commercial logging started already in the early 20th century (Kummer, 1992). Conversion of forest into grassland did not only result in drastically reduced biological diversity, including potential seed dispersers (Corlett, 2001), but also in a loss of natural resource management options for rural populations (Turvey, 1994; Appanah 2003).

Earlier attempts in the Philippines to reforest these largely unproductive ecosystems, often using exotic species, failed in most cases for ecological or socio-economic reasons (Quimio, 1996). In very vast degraded areas, systematic reforestation attempts have not been undertaken, because of too high costs. Quite recently, more cost-efficient methods have been developed, which aim to accelerate the natural process of succession, instead of establishing plantation-like systems (Dalmacio, 1991; Turvey, 1994; Lamb & Gilmour, 2003). These methods require only relatively few manpower and financial input, but call for an ecological understanding of the natural succession processes in the system (Hardwick *et al.* 2004). Of particular importance is the knowledge on factors supporting or preventing recruitment of woody vegetation in degraded areas. A precondition for recruitment of tree seedlings in grasslands is seed dispersal, which depends on frugivorous vertebrates in most of the tree species of tropical forests.

On the other hand, certain animal species feed on seeds (seed predators) and may be one of the factors which prevent or reduce the establishment of trees. Whereas seed dispersal into degraded areas has received considerable attention in the last years, the impact of seed predation on seedling recruitment is still widely unclear. Murid rodents of temperate zones are known to cache seeds for later consumption and consequently acting as seed dispersers, a behavior only rarely documented for tropical species (Hoch & Adler 1997). Particularly small seeds may pass the digestive tracts undamaged, and again murids might play an unexpected role in dispersal, particularly of pioneering species (Magnusson & Sanaiotti 1987).

In this study we investigated, how vertebrate frugivores influence recruitment of woody plants across a forest-grassland ecotone in the coastal plain of southern Palawan, Philippines through (a) seed dispersal and (b) seed predation.

Study area and methods

Palawan is located on the Sundaland continental shelf between Borneo and the 'oceanic' Philippines. The potential natural vegetation of the lowlands is a semi-deciduous tropical lowland rainforest. Palawan's climate is affected by monsoons, resulting in a pronounced dry season from December to May, and a less pronounced rainy season during the remaining months (Madulid 1995). The study area was situated in the coastal plain in the south-central part of the island. Most of this area has been cleared through logging and for agriculture starting in the 1960s. However, large parts have proven unproductive and were subsequently abandoned. This resulted in a mosaic-like cultivated landscape, with mostly rice paddies, tree plantations, patches of secondary and residual forests and pure grasslands dominated by *Imperata cylindrica*. Although burning and grazing were widespread, these impacts did not occur in the study site for the last eight years prior to the study.

Three transects of 55 m length each were established perpendicular to a forest edge, spanning 25 m into the interior of a secondary forest and 30 m into open grassland. Twelve stations were demarcated five meters apart from each other, starting from the forest edge, which resulted in five stations per transect in forest, one at the forest edge and six in grassland.

At each station, three plots of one square meter each were established; one centered on the transect and one each in two meters distance left and right of the central plot. All seedlings of woody plants, defined as regeneration less than 30 cm high, were counted in each plot, prior to the beginning of the experiments. Two aspects of seed distribution along the transects were studied:

Seed dispersal

Seed traps were used to assess seed deposition through birds, fruit bats and wind (Martínez-Garza & González-Montagut 2002; Ingle 2003). One seed trap was placed at the center of each station. It consisted of a metal ring which was elevated off the ground by circa 30 cm with bamboo pegs. The trap itself consisted of funnel-shaped nylon cloth which was attached with Velcro to the metal ring covering one square meter. The center of the cloth was weighted down with a stone to avoid seeds being blown out by wind. The mesh-size was fine enough to retain even the smallest seeds, but allowed rain water to seep through. Seeds including all debris in the traps were collected every ten days for one year and twenty days, sun dried and stored separately in plastic bags. Kernels of silica gel were exposed in the traps to estimate loss of already trapped seeds. Samples were separated from debris using sieves with different mesh sizes, forceps and a table lens with five times magnification. Debris was checked for adhering seeds. Samples were weighed with a mechanical precision balance and stored in pergamin envelopes.

Seed predation

Removal rates of artificially exposed seeds in baiting sites were used to assess levels of seed predation (Kollmann 1994). Murid rodents (Muridae), quails (Phasianidae) and buttonquails (Turnicidae) were assumed to play the most important role among the vertebrate secondary seed predators (those preying on seeds after their dispersal away from the mother tree) in the study area, given the scarcity of most avian candidates (parrots, large phasianids). Three bait sites were established per station, each consisting of two plastic trays with a diameter of 20 cm. Drainage holes in the trays allowed rain water to dissipate, and a central nail was used to fix the tray to the ground. One of the trays at each bait site was covered with a wire cage of 1 cm mesh-width to exclude vertebrate seed predators, but not insects. These were established to distinguish between seed losses from vertebrates and invertebrates. Twenty seeds of *Guioa pleuropteris* were exposed in each of the covered and uncovered trays. The seeds of this tree species are black, have a diameter of ca. 4 mm and were easily discernible in the trays. Five kernels of silica gel were added in each tray to determine losses unrelated to seed predation. After baiting, the sites were monitored daily for twenty days, and number of days until more than 50% of the seeds were removed was recorded. If at least ten seeds remained after termination of the experiment, this was noted as twenty days.

Correlations between seedling density, seed precipitation and seed removal rate were analyzed with Spearman's rank correlation coefficient using PAST software package (Hammer *et al.* 2002).

Results

Density of seedlings was highest in the forest stations averaging 12.9 (±2.14) seedlings per square meter. Numbers of seedlings ranged from 0 to 83 per square meter. Density of woody plant seedlings at the forest edge station averaged 4.3 (±1.54) individuals per square meter, ranging from 0 to 14. In grassland, density was considerably lower with 0.9 (±0.29) individuals per square meter on average, ranging from 0 to 11 (Fig. 1). However, 40 out of 54 grassland plots did not contain any seedlings of woody plants at all.

A total of 1,367 seed samples were collected from 36 seed traps. Highest seed rain was observed in the forest stations (Fig. 1). Most trapped seeds were tiny, around one millimeter in diameter. Only very few seeds (3.1%) showed adaptations to wind dispersal through surface enlargement.

Overall seed rain was low in terms of weight. It averaged 0.61(±0.06), 1.02 (±0.25) and 0.15 (±0.02) g per 10 days in forest, forest edge and grassland stations respectively. Whereas only 11.6% of the seed traps in forest stations did not contain seeds, 44.3% of the grassland traps were empty. Of the silica kernels, 81% could be retrieved during the sorting of the seeds, so that actual numbers of seeds deposited might be about one fifth higher than suggested by seed trap results.

Seed predation was most intense at the forest edge, where it took only 2.4 (± 0.53) days on average for the removal of more than 50% of the exposed seeds. It was also high in grassland were it took 4.1 (± 0.37) days on average until more than half of the seeds were removed, but gradually increased again with distance to the forest edge. The lowest removal rate with 10.1 (±0.84) days was recorded in the forest stations (Fig.1). Four stations in the forest contained more than half of the exposed seeds after the 20 days of the experiment.

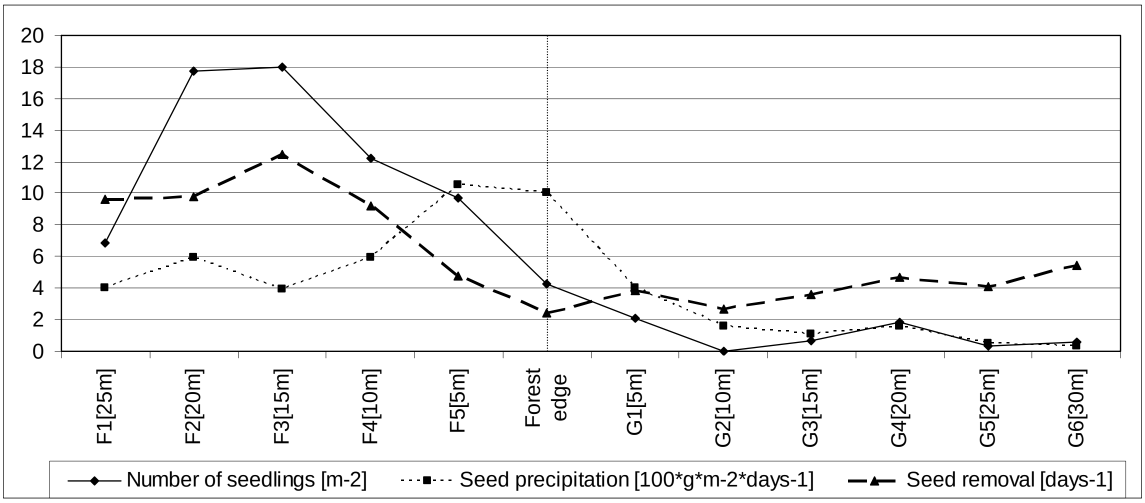

Figure 1 Seedling densities, seed precipitation and seed removal along the forest-grassland ecotone in the coastal plain of southern Palawan, Philippines. **F**: forest stations, **G**: grassland stations. Figures in parentheses indicate distances to forest edge.

Seeds in cages showed losses averaging 5.5% (±0.41) for all stations, not considering two cages which were completely overturned by unknown animals. The seeds retrieved from cages were all undamaged and did not show any signs of insect attacks. Ants were observed in the research site carrying away small seeds of *Melastoma* sp. and *Ficus* spp. This behavior could not be observed for the relatively heavy seeds of *Guioa pleuropteris*.

We found a significant correlation between density of woody seedlings and intensity of seed rain (r_s=0.69231; $p<0.05$), implying that recruitment was highest were seed rain was densest. Correlation between density of woody seedlings and removal of seeds from bait sites is significant (r_s=0.6993; $p<0.05$), indicating that establishment of seedling is highest, where seed predation is low.

Discussion

The most commonly discussed limiting factors for the successful establishment of tree seedlings in grasslands are unfavorable microclimate, competition with grass or herbaceous species, too much or not enough light, fire, grazing, seed predation, and limited density or activity of seed dispersers in degraded habitats (Goldammer 1993; Turvey 1994; Nepstad *et al.* 1996; Duncan & Chapman 2001; Hardwick *et al*. 2004).

Frugivorous vertebrates influence recruitment of woody plants across the forest-grassland ecotone in Palawan. In the research site, 69 species of birds, 16 mammals and 2 reptile species (batagurid turtles) were recorded which at least occasionally consume fruits (Widmann unpubl. data). Most of these, but particularly the more specialized frugivores, have their major distribution in forests. For many bird species, particularly pigeons (*Treron*, *Ducula*), bulbuls (*Pycnonotus*) and flowerpeckers (*Prionochilus, Dicaeum*), forest edges held a special attraction, possibly due to the high number of fruiting shrubs which can not persist under the closed canopy of the forest interior. This might explain the dense seed rain in seed traps placed at the forest edge. Galetti *et al.* (2003) noted that acceptance of artificial fruits through birds in semi-deciduous forests in Brazil was significantly higher along edges compared to the forest interior.

According to field observations in the study area, only few frugivorous bird species, particularly bulbuls and flowerpeckers, but all fruit bat species readily move into degraded areas, which is reflected in the seed precipitation of zoochorous (animal-dispersed) plant species recorded in grassland seed traps. Although density of seed rain in grassland is rapidly decreasing with distance to the forest edge, dozens of seeds are deposited every year on each square meter several tens of meters away from the forest edge. This large number of seeds obviously does not contribute to recruitment of woody plants. Other limiting factors, such as unsuitable microclimate, competition for light, water or nutrients (Widmann, unpubl. data) might be responsible for the extremely slow succession in these situations.

Similar studies from other tropical or subtropical regions show that other factors than seed dispersal account for low recruitment of tree seedlings in degraded areas. Sarmiento (1997) demonstrated that competition with tussock grass and not seed dispersal was the limiting factor in the succession of abandoned pastures close to forests in Ecuador. Similarly, Martínez-Garza & González-Montagut (2002) showed that competition and unfavorable microclimate were the limiting factors in the succession of abandoned pastures in Mexico. Single pioneering woody species in open land could however create conditions suitable for the establishment of additional woody species and serve as 'succession facilitators', like *Cordia multispicata* in Amazon pastures (Vieira *et al.* 1994) or *Psidium guajava* in Ecuadorean pastures (Sarmiento 1997; Zahawi & Augspurger 1999).

Density of seed rain can significantly increase under isolated trees (Guevara & Laborde 1993; Toh *et al.* 1999; Carrière et al. 2002) or snags serving as perches for birds (McClanahan & Wolfe 1993) within degraded areas. There are indications, however, that most of the seeds deposited do not find favorable conditions for germination. Under perches in a former mining site in Florida, only 0.06% of the seeds survived to become seedlings (McClanahan & Wolfe 1993).

Among the mammalian seed predators, four murid rodent species were most commonly recorded in the study area and most likely contributed to the loss of seeds. Two of these, the endemic *Maxomys panglima* and the non-native *Rattus exulans* were regularly trapped in grasslands (Widmann, unpubl. data). Among the bird species, *Coturnix chinensis* and *Turnix suscitator* were secondary seed predators which were common in grassland, but virtually absent in forest.

It has been demonstrated that bird species may play a role as seed predators in degraded forest systems in the neotropics (Pizo & Viera 2004). However, no studies are known to the authors on the impact of seed predation by ground-living grassland birds, particularly quails (Phasianidae), buttonquails (Turnicidae) or rails (Rallidae) which locally occur in high densities in grasslands of Sundaland.

Although rodents are particularly well-known secondary seed predators, the actual impact on recruitment is not well documented (Crawley 1992). An exception is a study from Kibale National Park in Uganda, where 44% of seeds protected with a cage germinated and survived as seedlings, whereas in unprotected stations, 98.7% of seeds or seedlings disappeared or were eaten (Duncan & Chapman, 2001).

In order to accelerate natural succession in degraded areas in close vicinity to potential seed sources, improvement of the survival rate of seeds (e.g. through creation of a suitable microclimate or reduction of competition) might lead to faster reforestation, compared to manipulation of seed disperser ensembles (e.g. through offering of perches). This could be achieved through the selective planting of so-called 'framework species', trees which are easy to propagate, able to suppress weeds and grasses and create a suitable microclimate for seedling establishment (Blakesley *et al.* 2002). A research priority for *Imperata* grassland in Sundaland would be to come up with a selection of tree species serving this purpose, as has been done for other parts of the tropics.

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