

別 紙

論文の内容の要旨

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論文題目 The ecological role of Asian elephants as agents of seed dispersal in human-dominated landscapes

(人為的環境下における種子散布者としてのアジアゾウの役割)

The Asian elephant (*Elephas maximus*) is one of the few remnant megaherbivores and the largest animal in Asian ecosystems. The extreme body size confers to Asian elephants unique functional properties and they are hence assumed to play an important role in ecological processes. In spite of this, little is actually known about this role. Asian elephants are endangered and have already disappeared from most of their historical range. Given this trend, it is urgent to understand their role in Asian ecosystems to evaluate the consequences of their local disappearance.

The aim of this PhD thesis is to contribute to the understanding of the ecological role of Asian elephants, particularly as agents of seed dispersal. Seed dispersal is a key process in the life cycle of plants with profound consequences for the structure and trajectories of plant populations and communities. Many plants rely on mutualistic interactions with animals to disperse their seeds, and Asian elephants have attributes to be efficient seed dispersers. Elephants eat large amounts of a broad diversity of plants, which can result in the dispersal of large quantities of seeds from a variety of plant species. Moreover, the combination of long gut passage times and wide-ranging behavior can result in a broad spatial scale of dispersal. The ecological flexibility of Asian elephants can result in strong context-dependency of their ecological role. Therefore, a variety of ecological scenarios must be considered to understand the role of Asian elephants in seed dispersal processes.

I present here four interconnected studies. First, I describe the food habits of Asian elephants in a mixed-deciduous forest of central Myanmar (Burma), with special focus on the plants potentially dispersed by them. Second, I describe the type of plants dispersed by Asian elephants in two dry monsoon environments of southeastern Sri Lanka, looking at the influence of landscape structure upon the type of seeds dispersed by elephants. Third, I describe the spatial scale at which elephants disperse seeds in the two previous environments and test hypotheses about the influence of behavioral and physiological factors on it. Finally, I study the role of Asian elephants on the dispersal of an invasive plant species in southeastern Sri Lanka comparing with that of other sympatric mammalian dispersers.

1. Food habits of Asian elephants in South East Asia

Little is known about the basic ecology, including food habits, of Asian elephants in South East Asia. This is partially due to the difficulty to study elephants living at low

densities in habitats with low visibility. In countries like Myanmar there are thousands of captive elephants living in semi-natural conditions that might be used as a proxy to study elephant ecology. I visited an elephant camp in central Myanmar and interviewed mahouts and veterinarians to describe the diet of captive elephants feeding on natural vegetation of a mixed-deciduous forest. Elephants showed a broad dietary breadth (103 plant species from 42 families); consumed mostly browse plants (94% of species); and were very selective about plant parts (e.g. many trees were eaten exclusively for their bark (22%) or fruits (14%)). I recorded the fruits from 29 plant species as eaten by elephants. I found several of these as fruit remains, seeds, or seedlings in elephant dung, suggesting that elephants play a role in seed dispersal in this environment. Work elephants and their mahouts proved to be a rich source of information to understand wild elephant ecology.

2. Seeds dispersed in Sri Lanka and the effect of landscape structure

Although frequently ignored, the ecological role of animals in seed dispersal is highly context-dependent. Human alteration of landscapes (e.g. forest fragmentation) can thus alter this role. I analyzed the species and quantity of seeds in the dung of Asian elephants at two locations of southeastern Sri Lanka. These areas differ in their landscape structure. Kotiyagala is a highly fragmented area in which the original forest has been largely replaced by grasslands; Mattala, on the other hand, is a relatively continuous scrubland. I collected approximately 30 dung samples per month for a period of one year in Kotiyagala but in Mattala sampling collection was interrupted after five months. I found seeds in most (93.5%, $N = 479$) of dung piles with an average of 1.6 (± 1.0 SD, max 6) species per sample. The seeds retrieved from elephant dung were categorized as 69 different plant species (only 14 present in both areas). I classified plants into four gross categories: (1) native woody and (2)

herbaceous plants, (3) invasive plants, and (4) crops. In the period of five months sampled in both areas there was an interaction between sampling area and the presence (frequency and abundance) of seeds in elephant dung. In the scrubland elephants dispersed native woody plants at higher frequency and quantities while in the fragmented area invasive and crop plants were far more common. This study shows the importance of human alteration of landscapes over the ecological role of animals, and uncovers a new form of conservation conflict — the spread of invasive plants by an endangered wildlife species.

3. Spatial scale of dispersal and factors affecting it

The digestive physiology and movement patterns of animal dispersers determine deposition patterns for seeds dispersed by endozoochory. I combined data from feeding trials, germination tests, and GPS telemetry of Asian elephants to (1) describe the spatial scale at which Asian elephants disperse seeds; (2) assess whether seasonal differences in diet composition and ranging behavior translate into differences in seed shadows; and (3) evaluate whether scale and seasonal patterns vary between two ecologically distinct areas — Sri Lanka's dry monsoon forests and Myanmar's mixed-deciduous forests. The combination of seed retention times (mean 39.5 h, max 114 h) and elephant displacement rates (average 1988 m in 116 hours) resulted in 50 % of seeds dispersed over 1.2 km (mean 1222-2105 m, max 5772 m). Shifts in diet composition did not affect gut retention time and germination of ingested seeds. Elephant displacements were slightly longer, with stronger seasonal variation in Myanmar. As a consequence, seed dispersal curves varied seasonally with longer distances during the dry season in Myanmar but not in Sri Lanka. Seasonal and geographic variation in seed dispersal curves was the result of variation in elephant movement patterns, rather than the effect of diet changes on the fate of ingested seeds.

4. Role of Asian elephants and other mammals mediating a plant invasion

The mesquite (*Prosopis juliflora*) is a leguminous tree from Central and South America that has been planted in tropical arid areas across the world, where it has frequently become invasive. Mesquite was introduced in Hambantota (southeastern Sri Lanka) in the early 1950s and has subsequently expanded, invading neighborhood areas such as Bundala National Park. I investigated the presence of mesquite seeds in the feces of Asian elephants and other two functional groups of dispersers (cattle and primates) at sites located at different distances from the current distribution of mesquite trees. I also analyzed the effect of consumption by these animals upon germination of mesquite seeds. Elephants were the only animals to disperse seeds at all the spatial scales considered; cattle (cows *Bos Taurus* and buffaloes *Bubalus bubalis*) dispersed the largest number of seeds although mostly at short distances; primates (grey langur *Semnopithecus entellus* and tokey monkeys *Macaca sinica*) dispersed few seeds only at short distances. Seeds consumed by cattle showed improved germination rate (28.3%) compared with control (17.0%) and seeds consumed by elephants (9.2%) and monkeys (4.5%). Germination time was increased by animal consumption — while control seeds stopped germination after 17 days, seeds consumed by animals continue to germinate three months after being planted. Animals enhance mesquite's invasion expanding its range and helping to colonize new areas (elephants) and consolidating current populations (cattle). Human management of wild and domestic mammals should take this into consideration.

This thesis is the most comprehensible study on the role of Asian elephants in ecological processes as well as one of the most complete studies regarding seed dispersal by a megaherbivore. Overall, elephants proved to be an efficient seed dispersal agent that consumed and dispersed large amounts of a broad variety of

plants, from different functional types, at long dispersal distances. The role of elephants as dispersers is context dependent, showing variations across seasons, geographical areas, and human alterations of landscape structure. Although elephants can play a positive role promoting forest maintenance and succession, their efficiency can also have a negative side e.g. promoting the spread of invasive plants.