SEED DISPERSAL AND FRUGIVORY IN TROPICAL ECOSYSTEMS

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Contents

Summary

This chapter first presents an overview of the seed dispersal cycle and then focuses specifically on seed dispersal. The distinctions between primary and secondary seed dispersal and factors that affect the efficiency and effectiveness of seed dispersal are presented. How mutualistic interactions between frugivores and fruits may be

recognized and definitions of fruit syndromes are described. Several methods for the study of seed dispersal are presented ranging from simple descriptive studies documenting seed dispersers, to more modern techniques that use genetic markers. Finally, this chapter concludes by discussing the possible consequences of the elimination of vertebrate seed dispersers from tropical forests.

1. Introduction

1.1. Definition of Seed Dispersal

Seed dispersal consists of the removal and deposition of seeds away from parent plants. Plants have evolved several different mechanisms of seed dispersal to achieve dispersal from the mother plant including anemochory (wind-dispersed), hydrochory (water-dispersed) barochory (gravity-dispersed), autochory (self-dispersal by explosion), and **zoochory** (animal-dispersed). **Zoochory** may be further divided into **exozoochory,** where the seeds are attached to the outside of the animal's body or **endozoochory**, when the seeds are swallowed and ultimately dispersed via defecation.

Of these seed dispersal mechanisms, **endozoochory** is the most important in tropical ecosystems. An estimated 51 to 98 percent of canopy and sub-canopy trees in Neotropical forests are vertebrate-dispersed; a similar estimate is found for the Paleotropics, with estimates ranging from 46 to 80 percent. Mammals and birds are the most important vertebrate groups responsible for seed dispersal in tropical regions. Bats and primates contain the most frugivorous species among mammals and are recognized as key taxonomic groups for seed dispersal in tropical forests. Other mammal groups that are documented to be primary dispersers as well include species from Carnivora, Rodentia, Proboscoidea, Perissodactyla and Artiodactyla.

1.2. Organization of this Review

In this review, we will first explain the seed dispersal cycle and highlight where seed dispersal fits into this scheme and patterns of primary and secondary dispersal in tropical regions. We will then discuss the importance of seed dispersal and mutualistic relationship between plants and their animal-dispersers. This section is followed by a description of different techniques used to study the phenomena of seed dispersal in tropical regions with case studies used to represent different methods. We close with a section that discusses the implications on seed dispersal of human alterations of vertebrate populations and the consequences this may have for the long-term maintenance of tropical forest diversity.

2. The Seed Dispersal Cycle

A distinction should be made between the *process of seed dispersal* (i.e. seeds are moved from parent plants) and the *seed dispersal cycle* which consist of a series of events beginning with seeds produced by parent plants and ending with the adult plant composition found within the forest (Fig. 1). Seed dispersal is only one step in the *seed dispersal cycle* which functions as a "demographic bridge" linking the end of the adult plant reproductive cycle with the establishment of their offspring.

Seed dispersal is first affected by the adult composition of tree species and their fruit availability. Fruit availability of any one species at a particular time of year depends upon successful pollination, and the flower and fruiting phenology of the species. Fruit removal by frugivores depends on many factors including diet choice, nutrition, competition with other frugivores, visitation and fruit removal rate, and frugivore behavior. Once seed uptake has occurred, actual seed dispersal depends on seed passage time in gut, disperser movements, disperser behaviors, scatter hoarding and seed caching. Seed rain or deposition depends on seed handling time by animals and seed predation. Germination depends on the availability of light, water and **gaps**, the existing seed bank, pathogens and fungi. Germination success will ultimately determine the seedling distribution within the forest. Seedlings will need to survive the same threats as seeds undergoing germination, in addition to **density-dependent mortality** in order to be recruited into the next generation of saplings and the next generation of adult plants (Figure 1).

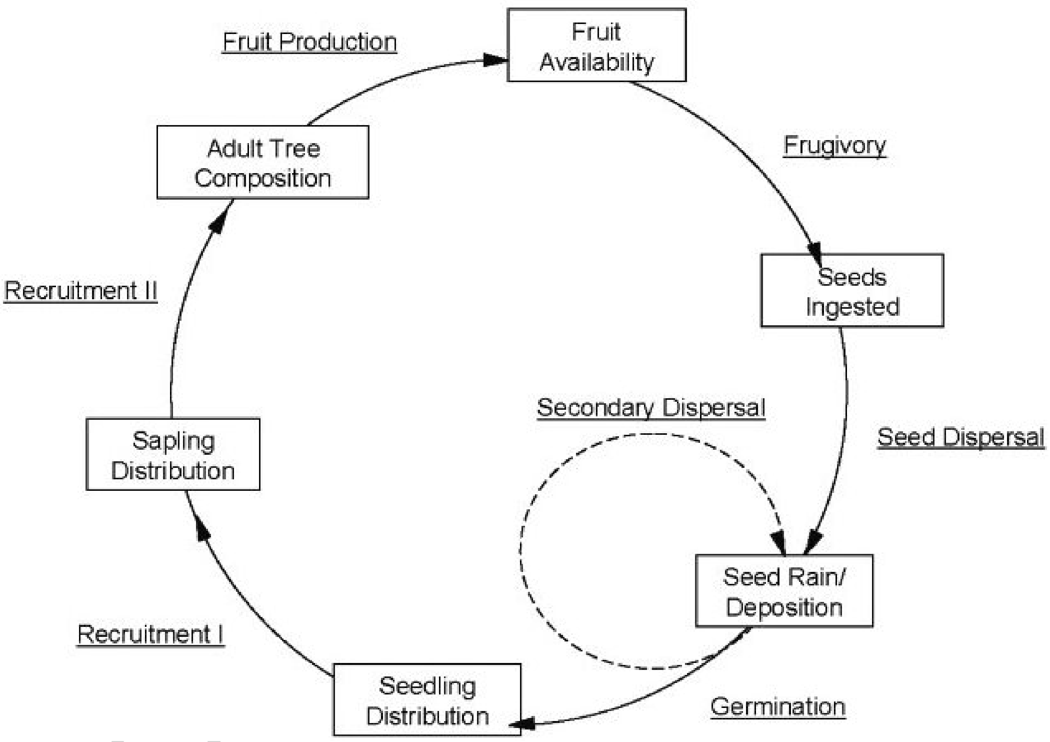

Figure 1: Seed dispersal loop figure from Wang and Smith 2002

2.1. Primary Dispersal

Primary dispersal consists of the removal of a fruit from a tree and the deposition of seeds from this fruit in a particular area. In addition to factors that affect frugivore choice that determine if a fruit is consumed or not, once the fruit is swallowed a series of factors affect primary seed dispersal and the ultimate fate of the consumed seeds. These factors include body size, digestive strategies, ranging behavior, and defecation of the frugivores. Larger animals can swallow bigger seeds than smaller ones. The time required for seeds to pass through the digestive tract affects the fate of swallowed seeds in that seeds that spend more time in the digestive tract are generally deposited at greater distances from the mother plant and frequently consist of one species. Animals with short gut retention times more often deposit seeds closer to the mother plant and usually create mixed species **seed shadows**. Furthermore, the action that occurs in the gut may promote seed germination success (higher velocity of germination or greater number germinated) or acids in the stomach may actually destroy the seeds making them nonviable. The distance that different animals move and their foraging pattern also affect the fate of primary dispersal. In general, animals that travel widely in a day will deposit seeds over a greater area than mammals that intensively exploit a smaller day range moving shorter distances. Finally, defecation patterns also affect seed dispersal, in that they may be deposited in high-density clumps, singly, or in low density clumps.

2.2. Secondary Dispersal

Secondary dispersal consists of the removal of seeds once they have been deposited by their primary disperser. Spit seeds and dropped, wasted fruit may be exploited by other seed dispersers such as, rodents, deer, and peccaries who may then serve either as secondary dispersal agents or seed predators. Some invertebrates like ants and dung beetles may also contribute to secondary dispersal of small seeds, but their effect on final seed germination and establishment is poorly known compared to that of mammals. The distance to which mammals secondarily remove seeds relative to parental trees varies significantly among species. For example, peccaries and tapirs perform long-distance seed movement (possibly up to 20 km), while small bodied mammals such as rodents move seeds much shorter distances (5-100 m).

Most rodents are granivores that prey on seeds; however, the two main foraging behaviors employed by many rodents, scatter-hoarding and larder-hoarding have different effects on secondary dispersal. In larder-hoarding seeds are usually buried more deeply and in fewer locations, while in scatter-hoarding seeds are buried less deeply and in several locations. Therefore, scatter hoarding often results in effective secondary dispersal and may contribute to seed survival when one of the following occurs: (1) the rodent forgets the location of a cache, (2) the rodent has a superabundance of seeds in several caches, and thus does not return to all of them, or (3) the rodent suffers mortality and fails to return to a cache. In contrast, larder hoarding rarely results in effective secondary dispersal because of the low probability of germination of seeds buried deeply.

3. Why Seed Dispersal Matters?

3.1. Seed Dispersal and Plant Diversity

The reward to the animals is quite obvious, food, but what do the plants get out of this mutualistic relationship? Seeds removed from parent trees escape from **density-dependent mortality** under their crowns, may colonize open habitats (succession), and/or experience directed dispersal to appropriate **microsites**, which allows escape from predators or enhances the establishment of seedlings. Although these factors are not mutually exclusive, the **Janzen-Connell escape hypothesis** is well supported (see Section 6.1). Recent work in Panama has unequivocally shown that density-dependent mortality — and its subsequent effect on seedling recruitment —increases tropical plant species diversity.

In the tropics, seed dispersal by animals (mostly bats and birds) is also a critical component of plant regeneration and diversity restoration processes in disturbed areas. Flying vertebrates are attracted by isolated trees in pastures and open habitats that they use as perch or feeding roost. This locally fosters seed deposition. Light-demanding pioneer plant species, adapted to the dry conditions of open habitats, will first emerge from this seed potential. They will produce a more shaded environment where shade-tolerant species will in turn develop and eventually replace pioneer plants.

3.2. Efficiency, Effectiveness, Quantity and Quality

Not all fruits that are removed and ingested by animals result in effective seed dispersal. The effectiveness of seed dispersal depends on both the quantity of seeds removed and the quality of dispersal. The main factors that affect the quality of dispersal are the distance moved from the parental tree, and the particular microsite the seed is deposited in. An efficient disperser (that disperses far or provides a well scattered seed deposition) may not be an effective disperser in that it does not deposit seeds in a suitable manner (e.g. clumped) or in a suitable place (e.g. in forest understory some seeds do not germinate because of lack of light). Some animals regularly result in poor seed dispersal because of **dispersal limitation**. Animals contribute to this phenomenon when they disperse seeds to feeding roosts (bats and birds), resting or sleeping sites (monkeys), latrines (rhinos and tapirs), caches (rodents) or fruiting trees (monkeys). In some circumstances, dispersal limitation is considered as a positive feature for the maintenance of plant diversity (see Section 6.4 for more information).

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Bibliography

Bascompte J. and Jordano P. (2006). The structure of plant-animal mutualistic networks. *Ecological networks* (eds. M. Pascual and J. Dunne), 143-159. Oxford University Press. [This reviews the way plant-animal networks, including dispersal networks, are structured].

Fenner M. (2000) Seeds: The ecology of regeneration in plant communities. 2nd edition (ed. M. Fenner), 125–165. CAB, Wallingford, England. . [A comprehensive book reviewing different factors affecting regeneration, including seed dispersal].

Forget P.-M., Lambert J.E., Hulme P.E. and Vander Wall S.B. (2005). *Seed fate: Predation, dispersal, and seedling establishment*, 410 pp. Cambridge, MA, USA: CABI Publishers. [This book provides a comprehensive review of several of the factors affecting seed dispersal].

Forget P.-M. and Vander Wall S. B. (2001). Scatter-hoarding rodents and marsupials: Convergent evolution on diverging continents. *Trends in Ecology & Evolution* **16**, 65–67. [This work shows how different organisms contribute similar roles in seed dispersal in different tropical regions].

Gautier-Hion A., Duplantier J.-M., Quris R., Feer F., Sourd C., Decoux J.-P., Dubost G., Emmons L., Erard C., Hecketsweiler P., Moungazi A., Roussilhon C. and Thiollay J.-M. (1985). Fruit characters as a basis of choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**, 324–337. [A review of frugivory and fruit syndromes in an African forest].

Herhey D.R. (2004). The widespread misconception that the Tambalacoque or Calvaria Tree absolutely required the Dodo bird for its seeds to germinate. *Plant Science Bulletin* **50**, 105–108. [A critical review of the Dodo-Tambalacoque mutualism hypothesis].

Hurtt G. C. and Pacala S.W. (1995). The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* **176,** 1–12. [This work shows the links between dispersal limitation and plant diversity].

Stoner K.E., Riba-Hernández P., Vulinec K. and Lambert J.E. (2007). The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. *Biotropica* **39**, 316–327. [A comprehensive review of the role of mammals in seed dispersal in tropical forests].

Stoner K.E., Vulinec K., Wright S.J. and Peres C.A. (2007). Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica* **39**, 385–392. [This work synthesizes information about the impacts of loosing mammal seed dispersers in tropical forests].

Wang B.C. and Smith T.B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**, 379–385. [A review of recent advances in fundamental and applied ecology of seed dispersal, including recommendations for experimental designs and future directions].

Biographical Sketches

Kathryn E. Stoner received the BS and MA degree from the University of Michigan and the PH.D. from the University of Kansas in 1993. She worked as Co-Director of Palo Verde Biological Station for the Organization for Tropical Studies in Costa Rica and worked teaching a variety of tropical biology field courses in Costa Rica for several universities (Pennsylvania State University, Duke University, University of Costa Rica). In 1998 she participated as the Invited Scientist during a field course in Costa Rica for the Special Interest Group of the Smithsonian Institute. During the last 10 years she has worked as a Researcher for the Centro de Investigaciones en Ecosistemas for the Universidad Nacional Autónoma de México (UNAM). She has participated as a subject editor of Biotropica since 2005. In 2004 she received the Sor Juana Ines de la Cruz award for outstanding excellence in research from UNAM. She has worked on different themes within tropical ecology in Costa Rica, Mexico and Brazil. Her interests include the effect of forest fragmentation on primates and bats and their consequences on forest regeneration (including seed dispersal and pollination), the evolution of color vision in primates, and bat-plant pollinator interactions.

Mickaël Henry completed the BS degree through an agreement between the Université de Rennes (France) and the Université du Québec à Rimouski (Canada), the MA degree from the Université de Sherbrooke (Canada) and the PH.D. from the Université Paris VI in 2005. His doctoral research focused on the functional consequences of landscape disturbances on the diversity of bats and of the seeds they disperse in tropical forest ecosystems. Since 2002, he has been involved in various research projects in French Guiana, Panama and Mexico in collaboration with the Muséum National d'Histoire Naturelle (Paris), the Centre National de la Recherche Scientifique (CNRS, France), the Universität Ulm (Germany), and the Universidad Nacional Autonoma de Mexico (UNAM). He is currently engaged in postdoctoral research at the Centro de Investigaciones de Ecosistemas (UNAM). His current research focuses on the ecology of interactions between frugivorous and nectarivorous bats and their plant resources.