Seed dispersal dynamics of a fleshy-fruited tree *Swida controversa* by various frugivorous animals

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Summary

Chapter 1

Seed dispersal has a profound impact on the fitness of plants. Among the various dispersal systems, many plants worldwide adopt endozoochory (seed dispersal via ingestion by animals). Endozoochorous plants often produce fleshy fruit to attract seed dispersers. These fruit are eaten and their seeds subsequently dispersed by a diverse range of animal taxa. Thus, understanding the seed dispersal interaction between fleshy-fruited plants and frugivores is important to understand the dynamics of plant population and community. In this study, I investigated the seed dispersal dynamics of a fleshy-fruited tree *Swida controversa* by frugivores in the Ogawa Forest Reserve, Ibaraki Prefecture, Japan. To evaluate various aspects of seed dispersal patterns, I adopted multiple methods: field observation, genetic analysis (identification of seed movement by SSR markers and seed disperser identification by DNA barcoding), and use of long-term monitoring data.

Chapter 2

The seed dispersal patterns of fleshy-fruited trees often show substantial seasonal and between-year variation due to temporal changes in frugivorous bird and fruit distributions. Elucidating such variation and how it affects plant regeneration is

important for understanding the evolution and seed dispersal maintenance strategies of these plants. In this chapter, I investigated the seed dispersal quantity and distance of *Swida controversa* for two years by field observation and genetic analysis. Early in the fruiting season, a short seed dispersal distance and a large quantity of fruit consumption by birds (seed dispersal quantity) was observed. In contrast, late in the fruiting season a long seed dispersal distance and a small seed dispersal quantity was observed. This relationship between seed dispersal distance and quantity may help to maintain constant seed dispersal effectiveness during the long *S. controversa* fruiting season. Between-year variation was also detected for both seed dispersal quantity and distance. More effective seed dispersal was achieved in the masting year as both seed dispersal quantity and distance were greater than that in the non-masting year. It is likely that the temporal variation in seed dispersal pattern revealed in this study plays a substantial role in the life history and population dynamics of *S. controversa*.

Chapter 3

Each frugivore species generates a unique seed dispersal pattern because of each species' distinct characteristics, such as movement pattern, seed retention time, and fruit preference. Thus, to understand seed dispersal of fleshy-fruited plants, the contribution of each frugivore to seed dispersal should be evaluated. In this chapter, to identify both the dispersers and the movement patterns of seeds of *S. controversa*, I conducted two types of genetic analysis: DNA barcoding of frugivore tissues and SSR genotyping of dispersed seeds. Differences in seed dispersal pattern between birds and mammals was detected. Seed dispersal distance by birds were short. Most seeds fell near or under the mother trees. Whereas, seed dispersal distance by mammals was significantly further

than that by birds. Dispersal distance by mammals (badger and raccoon dog) was greater than 50 m for all the seeds. Additionally, it was not possible to identify the maternal trees of approximately two thirds of seeds, indicating that these seeds were from outside of the plot. These mammals likely have a significant contribution as long-distance seed dispersers to the seed dispersal of fleshy-fruited trees.

Chapter 4

Large between-year variations.in the seed dispersal patterns of fleshy-fruited trees are common. However, most of the previous studies were based on observations over one or a few years, which may detect only part of the various seed dispersal patterns and mislead conclusions. In this chapter, I evaluated seed dispersal pattern of *S. controversa* and its between-year variation by using long-term seed trap data over twenty-two years and monitoring data of fruit removal by birds over four years. Large between-year variation was detected in all the considered factors: removal rate, timing of removal, and dispersal distance. Generalised linear models showed that the most effective dispersal was achieved in the years when both large crop size and late fruiting phenology was recorded. In such years, fruit persisted until transients and winter migrants, especially *Turdus* spp., arrived at the study site, resulting in large-quantity and long-distance seed dispersal by these migrants.

Chapter 5

My series of studies revealed the seed dispersal dynamics of the frugivore-dispersed tree *S. controversa* by unifying the results of field observation, genetic analysis, and long-term monitoring. *S. controversa* achieves a flexible seed dispersal

system by having a long fruiting season and fruit characteristics preferred by a variety of frugivores. By applying the approaches of this study to a wide range of studies on seed dispersal, we can understand the seed dispersal dynamics of frugivore-dispersed trees at a community level and increase our knowledge of forest demography, conservation of ecosystems, and the evolution and maintenance of mutualism.