Effects of Forest Fragmentation on Tree Regeneration from Bird-Dispersed Seeds in a Temperate Forest in Japan

Shoji Naoe[1], Shoko Sakai[1], Ayako Sawa[2], Takashi Masaki[3]

[1] *Center for Ecological Research, Kyoto University, Hirano 509-3, Otsu, 520-2113, Japan*

[2] *Graduate School of Life and Environmental Sciences,*
University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

[3] *Forestry and Forest Prodcuts Research Institute, Matsunosato 1,*
Tsukuba, Ibaraki 305-8687, Japan

Introduction

The loss and fragmentation of natural habitats caused by human activities are pervasive phenomena in terrestrial ecosystems and are considered to be major threats to biodiversity (Fisher & Lindenmayer 2007). Today, habitat fragmentation has become one of the most important research themes in conservation biology. With increased levels of research, our understanding of the processes involved in fragmentation and the effects of fragmentation on habitats has developed considerably over recent decades (Hobbs & Yates 2003). Important research advances include results from long-term fragmentation experiments (e.g., Bierregaard et al. 2001), the elucidation of the variety of effects caused by the creation of edges between fragments and surrounding altered land (e.g., Laurence 2000), and detailed considerations of the genetic and demographic consequences of fragmentation (e.g., Young & Clarke 2000; Isagi et al. 2007) and the alteration of plant–animal interactions, especially in plant reproductive processes (e.g., Aguilar et al. 2006).

Despite these advances, we are still a long way from developing a comprehensive conceptual framework for how forest fragmentation influences community composition, species diversity, and the dynamics of individual species (Hobbs & Yates 2003) for several reasons. First, the effects of fragmentation strongly depend on the characteristics of the focal ecosystem and the type of fragmentation (area, surrounding conditions, etc.). We cannot apply results for a tropical forest to a temperate forest, or those from a primary forest to a secondary forest. Fragmentation caused by land-use changes from forest to tree plantation may be entirely different from that caused by the expansion of agricultural lands. Second, many observations and experiments report changes after fragmentation or differences between continuous and fragmented forests, but it is difficult to provide clear insights into the ecological mechanisms of the changes or differences. Third, many studies examine only one or a few aspects of effects of the fragmentation. For the consideration of the long-term and total effects of forest fragmentation on biodiversity and ecosystem functions, pervasive studies of all biological processes of a species or forest are essential. In the case of plants, studies of the effects on reproductive processes such as pollination are abundant, whereas few studies have examined the effects on seedling survival and growth (Hobbs & Yates 2003).

Therefore, we investigated the effects of habitat fragmentation in a community of trees that use birds for seed dispersal in temperate forests in Japan. Although most dominant tree species in temperate forests are wind-pollinated and wind-dispersed, bird-dispersed tree species (which are mainly pollinated by insects) are important because they provide food for birds and mammals, play important roles in forest regeneration and forest succession, and maintain high species diversity. We monitored several biological processes using various methods in these forests: species composition in permanent plots; fruiting and dispersal using seed traps; the activities of seed dispersers by observing birds; and seedling germination and demography in permanent plots. Here, we report preliminary results.

Methods

Study site

The study was conducted in a mixed deciduous forest, the Ogawa Forest Reserve, at the southern edge of the Abukuma mountain region, central Japan (36º56' N, 140º35' E; 600–660 m above sea level). The reserve consists of a mixed deciduous old-growth forest of 98 ha (conserved forest) and remaining strips of old-growth forest approximately 50 m wide (fragments), surrounded by evergreen conifer plantations, secondary forests, and agricultural lands (pastures and vegetable or paddy fields; Fig. 1). The annual precipitation is approximately 1750 mm, and the mean annual temperature is 9.0°C, with an average monthly temperature range of –1.6°C in February to 20.5°C in August.

In the conserved forest, the total basal area and density of trees > 5 cm in diameter at breast height (DBH) were 33 m^2 ha^{-1} and 850 stems ha^{-1}, respectively (Masaki et al. 1992). The dominant tree species in terms of total basal area were *Quercus serrata* (27%), *Fagus japonica* (20%), and *F. crenata* (9%). Dwarf bamboos (*Sasa*, *Sasaela*, and *Sasamorpha* spp.) covered parts of the forest floor. Disturbances related to human activity, grazing, and fire, affected the forest until the 1930s, especially at the margins of the forest reserve (Suzuki 2002). The fragments are similar in composition and structure to the old-growth forest; however, they are small in area because large parts of the old-growth forest were cut during the 1970s and were converted into conifer plantations. The plantations are pure stands of *Cryptomeria japonica* or *Chamaecyparis obtusa*. The remaining area is covered by secondary forests and agricultural fields. The secondary forests have been managed for the production of firewood and charcoal for several decades. The dominant secondary forest species are *Q. serrata*, *Pinus densiflora*, and *Carpinus turczaninovii*.

Monitoring of plants

A 6-ha permanent plot (200 x 300 m) was established in 1987 in the central part of the Ogawa Forest Reserve (Fig. 1). The plot has been censused regularly for factors such as light, topography, and tree demography and growth within the plot (Tanaka & Nakashizuka 2002). In addition, we established two 1-ha plots in the fragmented forest area in 2006 (Fig. 1). All trees with DBH > 5 cm were measured, identified, and tagged. The plots in the conserved forest and the fragment have 1 x 1 m quadrats located at every 10 x 10 m grid point (total: 651 quadrats in the conserved forest and 132 in the fragment). In July 2006 and July 2007, we marked and monitored all current-year seedlings of bird-dispersed species in the quadrats. Seedling survival in 2006 was censused in October. To monitor seed rain and seed dispersal, we placed 329 and 67 seed traps at regular spacing in the plots of the conserved forest and the fragment, respectively. Seeds of bird-dispersed species were collected from the seed traps twice a month from July to December 2006 and identified to species. Seeds that were still covered with fleshy parts such as the mesocarp or aril probably dropped without being dispersed by birds; therefore, seeds that had lost the fleshy parts after being eaten and excreted by birds were distinguished and counted separately.

Monitoring of birds

To assess numbers and composition of bird dispersers, we conducted bird censuses within the plots and in an additional census site in the fragment from July to December 2006. We counted and identified birds passing through a 40 x 100 m area within a 15-min period. Each census was conducted early in the morning (first 3 h after dawn) and repeated three times at different points in the conserved forest and the fragment to obtain data for each census, except for three of the censuses in the fragment, which were only conducted twice. The censuses were done two to ten times a month, and more censuses were done in the bird migration season. In total, 33 censuses were completed in 2006. Frugivorous birds, which were the potential dispersers, were identified based on the literature (e.g., Kiyosu 1966; Kanouchi 2006). Differences in the densities of bird dispersers between the conserved forest and the fragment were examined using analysis of variance (ANOVA), with month and site as dependent variables.

Results

We compared the basal area of bird-dispersed woody species between the conserved forest and the forest fragment. For the bird-dispersed species *Prunus grayana, Ilex macropoda,* and *Eleutherococcus sciadphylloides*, the basal area in the fragment was more than twice that in the conserved forest (Table 1). The difference was especially large in *E. sciadphylloides*, at 9.3 times.

We compared the relative seed production per unit tree basal area for the three bird-dispersed species *Prunus verecunda, I. macropoda,* and *E. sciadphylloides,* for which > 30 seeds were trapped (Table 2). In all three species, the relative seed production was greater in the fragment than in the conserved forest, and the differences were significant. In contrast, the proportion of seeds dispersed by birds tended to be lower in the fragment than in the conserved forest, except for the liana *Rhus ambigua* (Table 3). The difference was significant for two tree species: *I. macropoda* and *E. sciadphylloides*.

We found 10 or more seedlings of at least 1 year old for six species in the two plots. The seedling densities of *E. sciadphylloides* and *Rhus ambigua* were considerably higher in the fragment than in the conserved forest in both study years. There was a significant difference in the survival of current-year seedlings only for *Cornus controversa*, for which the numbers were higher in the fragment than in the conserved forest (Table 4).

The number of bird species, frugivorous species, and bird diversity measured by the Shannon diversity index (H') did not differ significantly between the conserved forest and the fragment (Table 5). The number of frugivorous individuals was slightly greater in the fragment than in the conserved forest.

Discussion

Although these preliminary analyses were mostly based on data obtained in a single year, and 2006 was a poor year in terms of seed production (T. Masaki, unpublished data), we did detect some potential effects of fragmentation on seed production, seed dispersal, and seedling survival. Considering the relatively large differences in the basal area of some of the tree species, these effects may have already caused differences in the species composition of mature trees in the 30 years since forest fragmentation. Laurence et al. (2006) similarly reported a significant increase in trees with a DBH of 10–20 cm along forest edges 22 years after fragmentation. These effects may be positive or negative, depending on the processes and species involved. Positive effects of forest fragmentation were observed in seed production per unit tree basal area (Table 2) and in seedling survival for some species (Table 4). In terms of plant species reproduction, Aguilar et al. (2006) found an overall large negative effect of forest fragmentation on pollination and plant reproduction that was probably caused by pollination limitation. Positive effects have rarely been reported (e.g., Aizen & Feinsinger 1994). Our contradictory results may have occurred partly because our fragment has relatively large forests in close proximity, and the pollinator fauna may thus be little affected. In addition, the edge effect may have improved light conditions within the fragment, resulting in greater resources available for reproduction. The location of the fragment, i.e., on ridges or close to roads and rivers, could also be responsible for the better light conditions.

Unlike pollination, few studies have investigated the effect of fragmentation on seed dispersal and seedling density. Farwig et al. (2006) reported a marginally lower density of frugivorous birds, but significantly higher seed removal in forest fragments than in continuous forests, probably because of the paucity of other available fruit resources. Some studies have measured declines in the density of birds or frugivores with fragmentation (e.g., Andrén 1994; Cordeiro & Howe 2003; Luck & Daily 2003). Others have reported that forest fragmentation results in edge effects, namely high rates of nest predation and parasitism near forest edges, that can threaten bird populations by reducing nesting success in the remnant forest habitats (Batáry & Báldi 2004; Hoover et al. 2006). Our bird censuses indicate that bird densities or activities were slightly higher in the forest fragment. However, considering the difference in the amount of fruit, which was higher in the fragment, the difference is relatively small and may explain the lower proportion of dispersed seeds in the fragments than in the conserved forest. One further important consideration is that it may be more useful to examine actual dispersal patterns, rather than simply comparing the proportion of dispersed seeds (Schupp 1993). Further analyses, by combining examinations of seed dispersal, germination, and seedling survival over more than 1 year, will be important.

Our preliminary results reveal the importance of edge effects on the regeneration of bird-dispersed tree species such as an increase in fruit resources associated with an increase in frugivorous birds leading to an improvement in the survivorship of seedlings. It is essential to have a complete life history of the area and its species to understand the total effects and long-term results of forest fragmentation. The susceptibility to the effects of fragmentation may vary among tree species. Contrary to tropical forests, which are dominated by animal-dispersed trees, many bird-dispersed tree species that occur in temperate forests are mid-successional species. These species may be more robust than tropical species in their responses to forest fragmentation.

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TABLE 1. Basal area of major tree species in plots in the conserved forest (6-ha plot) and forest fragment (two 1-ha plots).

	Basal area (cm^2/ha)	
Species	Conserved forest	Fragment
Bird-dispersed plants		
Prunus verecunda	9249	4266
Prunus grayana	508	1632
Ilex macropoda	1020	2419
Cornus controversa	13411	9737
Eleutherococcus sciadphylloides	805	7512
Kalopanax septemlobus	7989	4027
Other plants		
Fagus crenata	29102	20904
Fagus japonica	63330	11615
Quercus serrata	93457	76164
Quercus crispula	11005	51239
Castanea crenata	15022	63890
Styrax obassia	8653	5421
Acer amoenum	12209	14411
Acer mono	11350	3708
Carpinus laxiflora	15108	19493

TABLE 2. Relative seed production per unit basal area in the conserved forest and the forest fragment in 2006. Tree species with 30 > seeds for both forests are included.

	Relative seed production (no./cm^2)	
Species	Conserved forest	Fragment
Prunus verecunda	0.016	0.020**
Ilex macropoda	0.067	0.094**
Eleutherococcus sciadphylloides	0.011	0.020**

**$p < 0.01$, chi-square test for independence.

TABLE 3. Comparison of seed removal rates between the conserved forest and forest fragment in 2006. Species with 30 > seeds for both forests are included.

Species	Conserved forest	Fragment
Prunus verecunda	0.17	0.15
Ilex macropoda	0.59**	0.44
Eleutherococcus sciadphylloides	0.53**	0.25
Rhus ambigua	0.52	0.66

**$p < 0.01$, chi-square test for independence.

TABLE 4. Density of current-year seedlings in July 2006 and 2007 in the conserved forest and forest fragment, and survival rates of the seedlings from July to October 2006.
Species with 10 > seedlings in either year are included.

	Seedling emergence (no./m^2)				Survival rate (Jul-Oct 2006)	
	2006		2007			
Species	Conserved forest	Fragment	Conserved forest	Fragment	Conserved forest	Fragment
Ilex macropoda	-	-	0.03	0.08	-	-
Cornus controversa	0.31	0.40	0.85	0.65	0.08	0.25**
E. sciadphylloides	0.07	1.09	0.07	0.89	0.57	0.41
Kalopanax septemlobus	-	-	0.57	0.19	-	-
Rhus ambigua	0.04	0.08	0.36	1.11	0.19	0.10
Euonymus oxiphyllus	0.26	0.13	0.40	0.05	0.4	0.29

**$p < 0.01$, chi-square test for independence.

TABLE 5. Comparison of the number and diversity of birds between the conserved forest and the forest fragment observed from July to December 2006.

	Conserved forest	Fragment
Number of bird species	26	27
Shannon diversity index (H')	2.64	2.58
Number of frugivorous species	22	22
Number of frugivorous individuals	283	344*

*$p < 0.05$, one-way ANOVA.

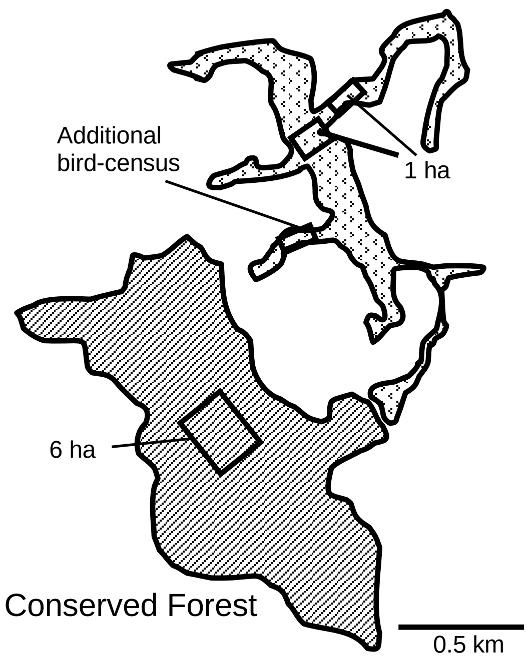

FIGURE 1. Location of plots and bird census sites in the conserved forest and the forest fragment in Ogawa Forest Reserve.