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Summary

In forests, maintaining and/or increasing biodiversity has become an increasingly important management goal to provide a broad array of ecosystem services that directly or indirectly benefit human endeavors. Although degradation of biodiversity is a worldwide concern on both global and local scales, relatively little evidence is available on the mechanisms of biodiversity. We focus on studies of mechanisms maintaining biodiversity (i.e., species diversity, genetic diversity) and ecosystem functioning.

Mechanisms of Species Diversity in Temperate Forests

In temperate forests, it was thought that species diversity is mainly created by abiotic factors, such as heterogeneity of light, water, and nutrients, each of which is closely related to topography and canopy gaps (Nagamatsu *et al.*, 2002 ; Seiwa *et al.*, 2006). However, increasing evidence indicates the effects of biotic factors such as pathogens and herbivores, both of which have an important role in maintaining species diversity in tropical forests. We tested the two most important hypotheses explaining species diversity of tropical forests in temperate forests.

Janzen and Connell hypothesized that seed dispersal enhances the probability of survival by distancing offspring from adults, because host-specific natural enemies reduce recruitment near conspecific adults in a density-dependent and/or distance-dependent manner, thereby freeing space for other plant species and generating species diversity within plant communities. Our community-level studies show that distance- and/or density-dependent juvenile mortality caused by pathogens and by invertebrate and vertebrate herbivores occur in most tree species co-occurring within a forest (Tomita *et al.*, 2002 ; Yamazaki *et al.*, 2009). These traits strongly suggest reciprocal replacement of tree species co-occurring within forest communities. We also found that death and growth reduction in a distance-dependent manner occur throughout the juvenile stages, from current-year seedlings to large saplings (height ~3 m) in *Prunus grayana*, probably due to severe attack by a leaf pathogen on juveniles. Because this leaf pathogen causes leaf-spot symptoms and subsequent leaf shedding in the early growing season, the photosynthetic ability of juveniles is strongly reduced, particularly beneath the adults (Seiwa *et al.*, 2008). The leaf pathogen was identified as *Phaeoisariopsis pruni-grayanae* Sawada, which infects many more seedlings of *P. grayana* than seedlings of the two other tree species tested in inoculation experiments, suggesting selective host preference. If pathogens attack all juveniles similarly, juvenile mortality of the focal species will occur even beneath heterospecific adults when the total juvenile density is high, suggesting no benefit of long-range dispersal from conspecific adults. Thus, for Janzen-Connell mechanisms, species-specific pathogens are more important than generalist pathogens. This evidence strongly suggests that the Janzen-Connell hypothesis is valid even in temperate forests.

In spatially heterogeneous environments, a trade-off between seedling survival in the forest understory and relative growth rate in gaps promotes the coexistence of plant species (trade-off hypothesis). In temperate forests, however, little support for this hypothesis has been found under field conditions, as compared to shadehouse experiments. An experiment over a large resource gradient in a temperate hardwood forest strongly supported the idea of light gradient partitioning (i.e., species coexistence ; Seiwa, 2007).

We also found that shade-tolerant species allocate more carbon to defense and storage and less to growth compared to shade-intolerant species (Imaji and Seiwa, in press). The ratio of condensed tannins to TNC pool sizes was usually higher in shade-tolerant species than in shade-intolerant species. Hence, shade-tolerant species preferentially invest more carbon in defense than in storage. Such a defense-biased carbon allocation pattern would be advantageous for a shade-tolerant species, allowing such a species to persist in the forest understory even where damage from herbivores and pathogens is costly. In contrast, shade-intolerant species preferentially invest more carbon in growth rather than defense, and invest similar amounts of carbon in storage as shade-tolerant species, ensuring establishment success in gaps, where there is severe competition for light among neighboring plants. These contrasting carbon allocation patterns may contribute to species coexistence across light gradients.

Mechanisms Maintaining Genetic Diversity in Temperate Forests

The availability of hyper-variable microsatellite DNA markers has greatly extended the possibility of analysis of genetic diversity, gene flow, and/or parentage assignment in natural forests. In a primary beech forest, current-year seedlings and adult trees of *Fagus crenata* were sampled for microsatellite analysis, and the spatial patterns of seed and pollen dispersal were investigated based on parentage assignment analysis. Seeds are dispersed near their maternal trees (average distance : 11 m), but the average pollen dispersal distance is greater than the seed dispersal distance ($>$33 m). Larger trees tend to produce more seedlings for both maternal and paternal parents. The analysis revealed not only the basic pattern of gene flow at a local scale, but also the relative fertility of individual trees and temporal changes in spatial genetic structure in the forest.

Forest fragmentation can cause reduced seed production and genetic erosion in future generations. To evaluate the effects of forest fragmentation on pollen flow, the seed set and genetic diversity of the resulting seeds were compared among *F. crenata* trees located within various local pollen donor densities. Although the seed-set data suggested pollen limitation, pollen flow over a long distance was effective in the low-pollen-donor-density populations of *F. crenata* in the study plot. The results draw attention to the potential reproductive ability of fragmented or low-density populations as core populations for future generations.

Reforestation with non-local seed sources may result in genetic disturbance and maladaptation to local environments. Therefore, it is important to use a local seed source within a seed transfer zone delineated by the phylogeography of the species being reforested. To determine the local phylogeographic pattern (genetic structure) of *F. crenata* in Miyagi Prefecture, the variation in chloroplast DNA and nuclear microsatellites was investigated for natural and planted populations. Furthermore, cpDNA haplotypes and growth performance were investigated in a planted population of the species to demonstrate the fitness advantages of local genotypes. As a result, at least three seed zones (conservation units) were indicated for *F. crenata* in Miyagi. Furthermore, the cpDNA haplotypes of the planted trees showed that half of the plantations were non-local and that some plantations have a higher risk of causing genetic disturbance to adjacent natural forests. A fitness advantage of local haplotype plants (home-site advantage) was demonstrated in the planted population of mixed origin by comparing growth performance between local and non-local plants. Our results indicate that the establishment of conservation units is necessary to conserve local genetic resources in this species.

In conclusion, although gene flow via seed is limited to a small area, long-distance pollen flow could be effective to maintain local genetic diversity, even in a fragmented forest. It is important to conserve remnant forests in each region to promote the fitness of local species while avoiding the transplantation of non-local species that may devastate local populations.

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