

## Evolution of the Genus *Camellia* Based on the Biological Interaction and the Historical Background

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The genus *Camellia* (Theaceae) is particularly prevalent in East and Southeast Asia (82-280 species). According to the Flora of China, there are 13 species in the sect. *Camellia*, of which 12 are found in China (11 being endemic), and only two species, *C. japonica* and *C. rusticana*, are found in Japanese islands. Since these two species are distributed at the northern limit of the genus *Camellia*, it is thought to have come from the continent and have speciated in Japan. Comparing the morphology, most species of *Camellia* have separated flower filaments, but the sect. *Camellia* species except for *C. rusticana* and *C. chekiangoleosa* have connected filaments, which indicates the bird-pollinated flower characteristics to keep a large amount of nectar. *C. japonica* blooms in the winter when insects are absent and must depend on bird pollination whereas other *Camellias* depend on both pollination, insects and birds. Therefore *C. japonica* might be the most adaptable species for bird pollination. On the other hand, *C. rusticana* has ancestral traits with not-connected filaments in the sect. *Camellia*. We hypothesized that the pollinator shift from insects to birds may have caused speciation from the ancestral genus *Camellia* to the sect. *Camellia*. Later, *C. rusticana* might get back to insect pollination to fit the snowy environment in Japan. Hence, this study aims to examine the speciation of Japanese *Camellias* based on pollinator shift by comparing the floral morphologies and the genetic differentiation of the genus *Camellia*. Next, we examined the demographic history of *C. japonica*, which is widely distributed in the Japanese archipelago, the Korean peninsula, and the coastal areas of mainland China and Taiwan. Through the above examinations, we discuss the evolution of the genus *Camellia* in Japan based on biological interaction and the historical background.

We compared their morphologies of leaf hypodermis, flower form, petal color, filament color, and filament color in the twenty populations and estimate quantitatively the differentiation. In the results, PCA analysis clearly distinguished between these species, and both petal and filament colors were also statistically different between these species. The floral traits of *C. japonica* such as filament connection rates, nectar, and sugar contents are one of the most adapted characteristics for bird pollination. The eight cpSSR and the genome-wide SNPs by MIG-Seq revealed largely congruent results indicating that the genetic structures are divided into 3; southern and northern *C. japonica*, and *C. rusticana*. The relationship between the three species including the related species in China was further inferred from the phylogeny generated by RAxML using SNP data. It was found that *C. chekiangoleosa* is the ancestral species and that *C. rusticana* and *C. japonica* are more related. However, demographic analysis, discussed below, reveals that the divergence date between *C. rusticana* and *C. japonica* is also older. The intraspecific genetic structure of *C. japonica* was investigated using ADMIXTURE 1.3.0, and the populations were divided into (1) mainly northern and (2) mainly southern populations in the Japanese archipelago, (3) Chinese and Korean populations, and (4) Okinawa and Taiwanese populations. Demographic analysis using DIYABC was carried out on the four populations in which hybrid individuals were excluded by ADMIXTURE predicted that the northern Japanese populations firstly differentiated from the southern Japanese populations, and then the Okinawa and Taiwan populations differentiated. Later, the Chinese and Korean populations returned to the mainland (the continent) from the southern Japanese populations. This result is consistent with the results of ENM. The optimum distribution of *C. rusticana* during the last glacial period was almost the same as that of the present distribution on the Sea of Japan, suggesting that *C. rusticana* is a relict species in Japan since before the glacial period. The northern population is the ancestral group as a relict in Honshu Japan. The results of this study could provide not only the evolutionary history of the species but also the population priorities that should serve as the focus for future management and conservation of these species.



**Photo.** White-eye feeding on camellia nectar