



## Original research article

Effects of forest fragmentation on the mating system of a cool-temperate heterodichogamous tree *Acer mono*

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## ABSTRACT

Pollination is a key process for reproduction and gene flow in flowering plants. Anthropogenic habitat fragmentation, however, can disrupt plant–pollinator interactions, and may have a negative impact on the reproductive success and population viability of entomophilous plants. Heterodichogamous plants containing protandrous and protogynous individuals within a population may be susceptible to habitat fragmentation due to a lack of available mating partners. In this study, we investigated the effects of forest fragmentation on the mating system in the heterodichogamous plant *Acer mono*, a major constituent of cool-temperate deciduous forests in Japan. Microsatellite analysis was applied to 212 adult trees and 17 seed families from continuous and fragmented forests. Dispersal kernel modeling using the neighborhood model indicated that pollen dispersal of *A. mono* was highly fat-tailed. The estimated parameters of the model suggested that the siring success of a pollen donor increased approximately fivefold, with a 100 cm increase in its diameter at breast height (DBH), and that disassortative mating was five times more frequent than assortative mating. The mating system parameters of each mother tree, outcrossing rate ( $t_m$ ), biparental inbreeding ( $t_m - t_s$ ), and paternity correlation ( $r_{pm}$ ) varied among sites and conditions, depending on the local density of potential pollen donors. Whereas *A. mono* was effectively outcrossed ( $t_m = 0.901$ ,  $t_m - t_s = 0.052$ , and the number of effective sires was  $1/r_{pm} = 14.93$ ) in the continuous forest, clumped trees within the fragmented forest showed increased biparental inbreeding and reduced pollen pool genetic diversity ( $t_m = 0.959$ ,  $t_m - t_s = 0.245$ ,  $1/r_{pm} = 1.742$ ) as a result of localized mating combined with spatial genetic structures. In contrast, the isolated trees had a higher selfing rate, but the pollen pool diversity was maintained ( $t_m = 0.801$ ,  $t_m - t_s = 0.022$ , and  $1/r_{pm} = 15.63$ ) due to frequent long-distance pollination. These results suggest that although pollen limitation following habitat fragmentation could result in negative genetic consequences, enhanced long-distance pollination across a fragmented landscape could partly compensate for this limitation depending on the degree of forest fragmentation.

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## 1. Introduction

Habitat fragmentation due to anthropogenic modification constitutes a major threat to biodiversity (Wilcox and Murphy, 1985). It is a complex process that not only affects the physical environment but also has impacts on the biological processes required for the persistence of a species (Murcia, 1995; Saunders et al., 1991). Pollination is a key process for seed reproduction in flowering plants and a major component of gene flow. For animal-pollinated species, the negative impacts

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of fragmentation are expected to be pronounced because these plant–animal interactions are susceptible to anthropogenic habitat disturbances (Aizen and Feinsinger, 2002; Hadley and Betts, 2012; Harris and Johnson, 2004; Winfree et al., 2009). A lack of effective plant pollination may therefore not only reduce reproductive success, but could also negatively affect the genetic diversity of the plant populations over time.

Over the last two decades, studies have investigated the effects of habitat fragmentation on the pollination and reproduction of animal-pollinated plants (reviewed by Aguilar et al., 2006; Eckert et al., 2010; Hadley and Betts, 2012). The use of genetic markers, which enables estimates of mating system parameters, has contributed to understanding mating-system responses in fragmented landscapes (Coates et al., 2007), and has confirmed that habitat fragmentation has had negative impacts on reproduction through pollen limitation and/or increased selfing (Aguilar et al., 2008; Eckert et al., 2010; Ghazoul, 2005; Hadley and Betts, 2012). However, the susceptibility of plant reproduction to fragmentation varies greatly, and under some circumstances, fragmentation has also facilitated outbreeding (Bacles et al., 2005; Dick et al., 2003; White et al., 2002). These differential responses have not been fully explored, but they have been attributed to a function of the plant breeding system, the life history, the pollination vector, and pollinator specialization (Aguilar et al., 2006; Harris and Johnson, 2004).

The plant breeding system determines the dependence of its reproductive success on the availability of pollinators (Aizen and Feinsinger, 2002; Bond, 1994). Self-compatibility may also be an important predictor, as self-incompatible plants are considered to be more susceptible to fragmentation than self-compatible plants because they obligately require cross-pollination for seed reproduction (Aguilar et al., 2006). However, plants exhibit a wide array of breeding systems ranging from complete selfing to outcrossing (Goodwillie et al., 2005; Lande and Schemske, 1985), and include complex breeding systems such as heterostyly and heterodichogamy (Barrett, 2002). Moreover, the role played by the variation of the plant breeding system in its susceptibility to fragmentation has not yet been fully explored.

Maples (genus *Acer*, family Sapindaceae), a major constituent of boreal forests in the Northern Hemisphere, are known to exhibit labile complex sex expression, including dioecy, heterodichogamy, and duodichogamy (Gleiser and Verdú, 2005). Heterodichogamy is a complex breeding system in which both protandrous and protogynous individuals coexist in a population (Renner, 2001). Although it has been reported for only 17 genera in 11 families of angiosperms (Renner, 2001), almost half of the *Acer* species show heterodichogamy (Gleiser and Verdú, 2005). Heterodichogamy in *Acer* is particularly referred to as heterodichogamous androdioecy because it occasionally includes a low proportion of male individuals.

We previously investigated the mating system of the heterodichogamous maple *Acer mono*, and revealed that heterodichogamy in this maple effectively avoided selfing and promoted mating between protandrous and protogynous individuals (disassortative mating) without obligate compatibility systems (Kikuchi et al., 2009). Seed reproduction in this mating system is presumed to depend on the availability of potential mating partners and thus may be susceptible to habitat fragmentation.

Our aim was to investigate the effects of fragmentation on the pollination process and the reproduction of the heterodichogamous maple *A. mono*. The effects of fragmentation on the seed reproduction of this maple have already been examined by Shibata et al. (2009), who observed increased rates of empty and immature seeds with increased isolation of the seed parents. Therefore in this study, we focused on the quality of seeds; i.e., the effects of fragmentation on mating systems from a genetic perspective. It was hypothesized that, although heterodichogamy would avoid selfing in *A. mono*, habitat fragmentation would have significant negative impacts on the reproduction of this maple, because a decline of compatible partners in forest fragments would reduce effective outcross pollination, and subsequently the genetic variation of pollen pools of its progenies.

In this study we conducted microsatellite genetic analyses on the adults and their progenies in continuous and fragmented populations of *A. mono*. We particularly examined the genetic structure of adult individuals, the mating patterns, and pollen dispersal kernels. The mating system parameters in the progeny populations were also analyzed. Paternity analyses and estimation of pollen dispersal kernels provided accurate estimates of contemporary pollen transfer. Multilocus estimation based on the mixed mating model (Shaw et al., 1981) and the correlated mating model (Ritland, 2002) are robust and informative tools to evaluate the mating systems in plant populations, including selfing rates, biparental inbreeding, and pollen pool diversity. Moreover, these mating-system parameters can be applied directly to conservation because they influence population genetic diversity over time (Breed et al., 2013; Neel et al., 2001). The genetic structure of the adult populations was not the main focus of this study, but it was an important determinant of the impacts on seed quality.

## 2. Materials and methods

### 2.1. Field data and sample collection

This study was conducted at two sites (OGW and FRG) in a deciduous broad-leaved forest (36°56–57′N, 140°35′E, 610–660 m a.s.l.) in the North Kanto region of Japan (Fig. 1). The OGW consists of a 12-ha (400 × 300 m) rectangular site located in a 98-ha continuous forest (the Ogawa Forest Reserve, Ibaraki Prefecture). The FRG is a forest fragment located nearby (in Fukushima Prefecture) interspersed with artificial conifer (*Cryptomeria japonica* and *Chamaecyparis obtusa*) plantations. It comprises about 29 ha, and consists of thin strips, 5–200 m in width and 500–1500 m in length, which are located mainly along the ridges and rivers. These forest sites are dominated by deciduous broad-leaved trees, including

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