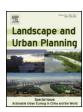
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Research Paper

Butterfly responses to cultivated field abandonment are related with ecological traits in a temperate Japanese agricultural landscape



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HIGHLIGHTS

- Cultivated fields have been abandoned at high rates in remote rural areas of Japan.
- Butterfly responses to abandonment of cultivated fields were examined.
- Specialist butterflies increased with increased proportion of abandoned fields.
- The responses of generalist butterflies to abandoned fields differ among species.
- Abandoned cultivated fields can be important habitats for butterflies.

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ABSTRACT

To examine the effects of cultivated field abandonment on butterfly assemblages, we investigated butterfly assemblages in seven local settlements with varying degrees of abandonment of cultivated fields. We hypothesized that species with specialist characteristics (univoltine and oligophagous species) would increase with an increasing proportion of old abandoned fields (50-80% of these fields had been abandoned for approximately 30 years) and that species that utilized annual plants would increase with an increasing proportion of recently abandoned fields (abandoned for one to two years). Species richness and the abundance of univoltine, oligophagous, and non-annual feeding species increased with increasing proportions of old abandoned fields, whereas those of multivoltine, polyphagous, and annual feeding species decreased or remain stable. Species that utilized annual plants did not respond to the amount of recently abandoned fields. Redundancy analyses showed that the proportions of old and recently abandoned fields affected butterfly assemblages but that other uncontrolled factors, such as road density and the distance to the continuous forests, did not affect butterfly assemblages. Our results showed that abandoned cultivated fields are beneficial to some specialist butterflies that are sensitive to the simplification of landscapes and can be an option for increasing biodiversity, particularly in simplified agricultural landscapes. Further research is required to reveal factors affecting vegetation types in abandoned cultivated fields, to determine the relative effects of local compared with landscape factors regulating butterfly assemblages, and to examine the role of abandoned cultivated fields compared with other semi-natural vegetation for conserving biodiversity in agricultural landscapes.

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1. Introduction

Since the mid-20th century, agricultural landscapes in rural areas have been increasingly abandoned worldwide because of economic and social changes (Cramer, Hobbs, & Standish, 2008; Fukamachi, Oku, & Nakashizuka, 2001; MacDonald et al., 2000). In the context of biodiversity conservation, ecologists have primarily focused on semi-natural open vegetation such as grasslands, meadows, and pastures because plants and insects inhabiting these habitats have markedly declined due to vegetation succession after

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abandonment (plants: Peco, Sánchez, & Azcárate, 2006; Pykälä, Luoto, Heikkinen, & Kontula, 2005; Uematsu, Koga, Mitsuhashi, & Ushimaru, 2010; butterflies: Choi & Kim, 2012; Erhardt, 1985; Nakamura, 2011; Pöyry, Lindgren, Salminen, & Kuussaari, 2005; Warren, 1987), although the importance of grasslands abandoned for 10-20 years has been recognized for butterflies (Balmer & Erhardt, 2000; Skórka & Lenda, 2010; Skórka, Settele, & Woyciechowski, 2007). However, in mountainous or hilly areas, cultivated fields have also been abandoned due to their remoteness, their physical or social disadvantages (e.g., low productivity and small, scattered farm plots), and to falling rural populations (Fukamachi et al., 2001; MacDonald et al., 2000). Because more than 10% of the cultivated lands are now abandoned in Japan and because the area of abandoned cultivated fields has doubled from 1990 to 2010 (MAFF Japan, 2011), the abandonment of cultivated fields is also assumed to significantly influence the biological communities of remote agricultural landscapes. However, although the effects of the abandonment of semi-natural open vegetation on insects, particularly butterflies, have been relatively well studied as mentioned above, the role of abandoned cultivated fields in conserving insect diversity has been poorly examined (however, see Skórka & Lenda, 2010). Apart from some plot-scale studies (Do et al., 2011; Ohwaki & Kaneko, 2013), our knowledge concerning the effects of the landscape-scale abandonment of cultivated fields have been quite limited, particularly in East Asia.

Effects of the abandonment of cultivated fields on insect assemblages have classically been studied in the context of the "habitat templet theory" developed by Southwood (1977), which predicted a shift in component species toward lower voltinism, a narrower host plant range, and lower mobility as vegetation succession proceeds. Many classical and recent studies have supported this theory: cultivated fields or early successional habitats (recently abandoned fields) consist of multivoltine, polyphagous, and mobile species, whereas relatively stable, late successional habitats (old abandoned fields) contain many univoltine, oligophagous and less mobile species of butterflies (Steffan-Dewenter & Tscharntke, 1997); moth (Alanen, Hyvönen, Lindgren, Härmä, & Kuussaari, 2011); homoptera (Brown & Southwood, 1983) and heteroptera (Brown, 1985; Frank & Kunzle, 2006). Butterflies are one of the beststudied insect groups, and their ecological traits are well-known in temperate regions (Öckinger et al., 2010). Furthermore, butterflies respond to differences in the landscape structure, particularly the proportion of semi-natural vegetation (Bergman et al., 2004; Weibull, Bengtsson, & Nohlgren, 2000), and butterfly responses to recent land use changes are highly related to the ecological traits of species (Kuussaari, Heliölä, Pöyry, & Saarinen, 2007; Nilsson, Franzén, & Jönsson, 2008). Therefore, butterflies are a suitable insect group to examine the effects of the abandonment of cultivated fields on a landscape scale in relation to their ecological traits. Butterflies observed in this study were grouped in terms of three ecological traits (voltinism, host plant range, and annual plant use) because information concerning these traits is available in Japan and because these traits are linked with vegetation succession and with human disturbances, such as cultivation (Kitahara, 2004; Steffan-Dewenter & Tscharntke, 1997).

The aim of this study was to test how the landscape-scale abandonment of cultivated fields affected butterfly assemblages in remote agricultural landscapes in Japan by comparing the butterfly assemblages among seven settlements, which had varying proportions of abandoned cultivated fields. We hypothesized that the species richness and abundance of specialized species (lower voltinism and a narrower range of host plants) would increase with an increasing proportion of abandoned fields, whereas the richness and abundance of species with opposite traits would decrease or remain stable. Species that can utilize annual plants were expected to increase particularly in young abandoned fields because young

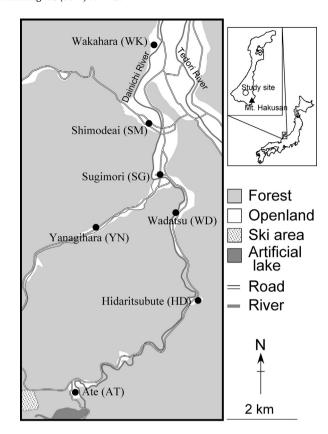


Fig. 1. Map of the study site showing the studied settlements.

abandoned fields usually have annual weeds (Southwood, Brown, & Reader, 1983). We also hypothesized that species with specialist characteristics could attain a high abundance in settlements with a higher proportion of abandoned fields. The potential of abandoned cultivated fields to conserve biodiversity in agricultural landscapes was discussed in relation to the ecological traits of species and to landscape structure.

2. Materials and methods

2.1. Study sites

The study area was in the Dainichi River Basin of the Ishikawa Prefecture in central Japan (36°17–36°22′ N, 136°34–136°37′ E). The Dainichi River is a tributary of the Tedori River and runs through rural and mountainous zones with many depopulated local settlements (old hamlets). We selected the following seven human settlements at altitudes of 165-290 m, which are listed from downstream to upstream: Wakahara (WK); Shimodeai (SM); Sugimori (SG); Wadatsu (WD); Hidaritsubute (HD); Yanagihara (YN); and Ate (AT) (Fig. 1, Table 1). Although four settlements (WD, HD, YN, and AT) are along the valley and the remaining three are in relatively flat areas, all were near the continuous deciduous-planted conifer mixed forests that cover the mountainous areas (Fig. 1). National census data in 1955 and 2005 showed that the human populations in the studied settlements ranged from 120 to 194 people in 1955 but dropped to 3-79 in 2005 (Table 1). Percentages of population decline (calculated as the human population in 2005 divided by the human population in 1955) were greater in the settlements in higher altitudes (AT, YN, and HD, Table 1) (Spearman's rank correlation: ρ = 0.93, P = 0.007, n = 7).

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