ORIGINAL ARTICLE

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Roles of riparian and secondary forests in maintaining the near-threatened butterfly, *Sasakia charonda* (Lepidoptera, Nymphalidae), populations in Japan

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Abstract To clarify the habitat requirements of the nearthreatened butterfly, *Sasakia charonda* (Lepidoptera, Nymphalidae), we studied the distribution pattern of its host trees, *Celtis sinensis* and *Celtis jessoensis*, and the utilization patterns of various vegetation types by this butterfly in the Oofukasawa River basin in Hokuto City, Yamanashi Prefecture, central Japan. Two species of host trees, *C. sinensis* and *C. jessoensis* (height = 2 m or more) were found in riparian forests on sandbanks (hereinafter, riparian forest), in forest regenerated after landslides on valley walls (landslide tracks), in secondary

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deciduous forests consisting mainly of Quercus acutissima or Quercus serrata and in forests established at abandoned paddy fields and their periphery, where weeds and shrubs used to be mown frequently to avoid shade on the paddies before their abandonment. This suggests that they are pioneer species, and their distribution and regeneration depend on natural and/or human disturbances. Host trees above 2 m were preferred by larvae, and there were very few such trees in secondary forests. More overwintering larvae occurred in riparian forests than at other sites. The number of S. charonda adults was highest at the edge of riparian forests, and we observed a variety of behaviors such as puddling, chasing and mating there. Although the number of adult butterflies was smaller inside and at the edge of secondary forests than in riparian forests, puddling by males and roosting on the trunk of Q. acutissima or Q. serrata by females were observed more frequently there than in riparian forests. Thus, we conclude that landscapes including both riparian forests with natural disturbance and secondary forests with *Quercus* trees are necessary to maintain host Celtis trees and S. charonda populations.

Keywords Secondary forest · Riparian forest · Sasakia charonda · Host tree · Disturbance

Introduction

To consider the conservation of animal populations, we need to understand the ecological conditions and requirements necessary for maintenance of the populations, not only at the ecosystem level, but sometimes at the integrated landscape level (Harris and Silva-Lopez 1992; Primack 1993, 1995; Hunter 1996; Meffe and Carroll 1997).

In Japan, the giant purple emperor, Sasakia charonda (Lepidoptera, Nymphalidae), is a symbolic insect known as the national butterfly of the country. At one time, the

species was very common in secondary broad-leaved deciduous forests almost all over the country. However, since the period of rapid economic growth, populations of this species have declined, mostly due to deforestation associated with changes in land use such as the construction of roads and buildings, and a decrease in the number of their host trees, Celtis sinensis and Celtis jessoensis (Higuchi and Sato 1987). Consequently, S. charonda is now designated as a near-threatened insect in Japan (Ministry of the Environment 2006). On the other hand, it is known that there are not many Celtis trees in the secondary forests managed for acquisition of firewood and charcoal, and therefore, the original habitat of S. charonda has not yet been clarified in detail (Kobayashi and Inaizumi 1999, 2000, 2002; Kobayashi and Inaizumi 2003a, b; Kobayashi et al. 2004; Kobayashi and Kitahara 2005a, b).

In modern-day Japan, secondary forests have largely been converted into conifer plantations. On the other hand, riparian and riverside forests have largely disappeared, and the nature of those that remain has changed considerably due to the construction of concrete dams, barriers and embankments to prevent flooding and landslides, and as a means to stabilize river environments (Johnson et al. 1976; Rood and Heinze-Milne 1989; Nakamura and Shin 2001; Takagi and Nakamura 2003). The regeneration of many tree species belonging to the family Ulmaceae is facilitated by natural disturbances (e.g., Matsuoka and Sano 2003). Thus, there is a possibility that the regeneration of C. sinensis and C. jessoensis belonging to the same family is related to river disturbances, and the populations of S. charonda using the trees are influenced by changes in the riparian environments.

In the present study, we aimed to clarify the role of riparian forests and secondary forests in the maintenance of *S. charonda* populations, and based on the results, to discuss a conservation strategy for the species. We focus on three questions: (1) Do populations of *C. sinensis* and *C. jessoensis* depend on natural riparian disturbances? (2) What are the requirements for maintaining a population of *S. charonda* at the landscape level? (3) What are the functional differences between riparian forests and secondary forests in maintaining *S. charonda* populations? To answer these questions, we carried out the analyses on tree distribution along with topography and land use, population censuses and behavioral observations of *S. charonda* in the various components of the landscape.

Life history of S. charonda

Sasakia charonda is distributed over the mountain regions of northern Taiwan, continental China, the Korean Peninsula and Japan. In Japan, S. charonda is univoltine, and the host trees are C. sinensis or C. jezoensis. On the Kanto Plain of central Japan, the flight season of adults extends from late June to late

August. The minimum duration of the egg stage is 5 days (Kobayashi and Inaizumi 2002). Larvae feed on leaves until the end of October, when they reach third or fourth instar. They descend on the trees early in November and overwinter in the litter near tree trunks. In early spring of the next year, they return to the budding trees, finish their development there and pupate in June.

Study area

Field studies were carried out in the Oofukasawa River Basin in Hokuto City, Yamanashi Prefecture, central Japan, which is one of the most well-known habitats of *S. charonda* in Japan (Fig. 1). Along the river, there were narrow flooded beds with several sandbanks existing (Fig. 2). The bedrock at this area consists of mechanically unstable volcanic deposits. There were steeply slanting valley walls on the left bank of the river, and

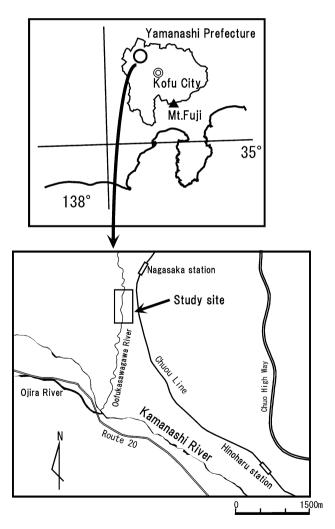
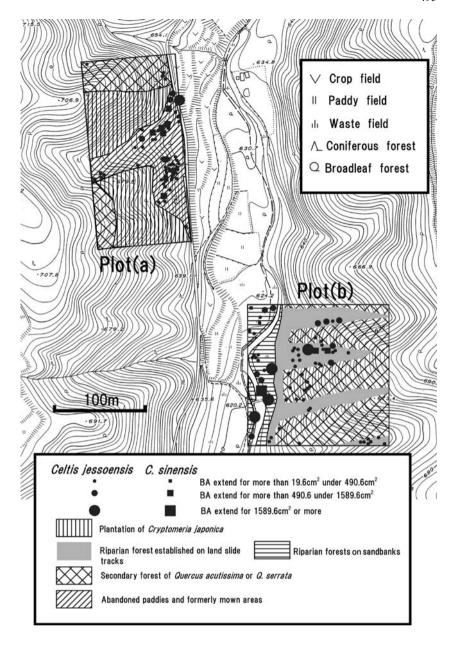


Fig. 1 The research area of this study was in the Oofukasawa river basin in Hokuto City, Yamanashi Prefecture, central Japan

Fig. 2 Land use map of the Oofukasawa river basin. BA extends for more than 19.6 cm², but less than 490.6 cm² (dbh extends for more than 5 cm, but less than 25 cm). BA extends for more than 490.6 cm², but less than 1,589.6 cm² (dbhs extends for more than 25 cm, but less than 45 cm). BAs extends for 1,589.6 cm² or more (dbh extends for 45 cm or more)



gentle slopes on the upper part of the walls. Shelves of paddies were mainly located on the right bank of the river and gentle slopes on the upper part. On the valley walls and sandbanks, there were riparian forests composed of trees such as C. sinensis, C. jessoensis, Juglans mandshurica, Zelkova serrata and Gleditsia japonica. On the gentle slopes of the upper parts, there were secondary deciduous forests composed of Quercus acutissima and/or Quercus serrata (secondary forests), or the plantations of Cryptomeria japonica. At the edges of some secondary forests and plantations of C. japonica, there were abandoned paddies and places where weeds and shrubs had been mown to avoid shading the paddies (formerly mown area). In abandoned paddies and formerly mown areas, young forests have already been established. The forests are mainly composed of C. sinensis, C. jessoensis, Carpinus tschonoskii, J. mandshurica and Z. serrata.

Methods

Landscape and host tree distribution

We classified the land cover in the basin into five types: (1) secondary forests, (2) plantations of *C. japonica*, (3) abandoned paddies and formerly mown areas, (4) forest established on landslide tracks, and (5) riparian forests on sandbanks. The different landscape types were mapped (1/2,500) using an area scale with dot grids S-II (Japan Forest Technical Association 1963).

In order to clarify their regeneration patterns of C. sinensis and C. jessoensis, we recorded the distribution of the two host trees. We established a research plot of 100 × 200 m (plot-a) in an area covering abandoned paddies and formerly mown areas to the secondary forests and C. japonica plantations behind them, and another plot of 150×150 m (plot-b) covering a sandbank and a valley wall with riparian forests to the secondary forests in the upper part of the wall (Fig. 2). In each plot, we counted all host trees whose height was 2 m or more and diameter at breast height (dbh) was 5 cm or more. We recorded species, location and dbh value. For the host trees branching off under breast height, we measured the dbh of all stems and obtained the total basal area (BA) as a measure of their size. We plotted their location on a map (1/2,500). The investigations were conducted during 9-13 June for plot-a and 11–13 September 2005 for plot-b.

In this paper, we treated *Celtis* spp. (*C. sinensis* and *C. jessoensis*; two species) as a single "species" of host tree in the calculations for dbh, BA and the number of larvae per host tree. They exhibit similar ecological characteristics, both are utilized as larval hosts and did not differ in the number of overwintering larvae as found in a related study (Kobayashi et al., unpublished).

Number of S. charonda larvae

Number of larvae on host sapling

On 8 October 2004, we randomly sampled 60 host saplings whose height was < 2 m each in secondary forests, abandoned paddies and formerly mown areas and riparian forests. Then we counted the number of larvae on the saplings. On 18 September 2005, we also randomly sampled 40 host saplings in secondary forests, plantations of C. japonica, abandoned paddies and formerly mown areas, forest on landslide tracks and riparian forests. We then counted the number of larvae on the trees in the same way as in 2004. The larvae were in the third to fourth instar when sampled.

Number of larvae on host tree

In 2004, we randomly sampled 40 host trees (height ≥ 2 m) each in secondary forests, abandoned paddies and formerly mown areas and riparian forests. We collected litter as carefully as possible at the forest floor within the range of 50 cm from the base of each host tree from 25 November to 8 December and counted the number of *S. charonda* larvae in our laboratory immediately after the sampling.

Also, in 2005, we randomly sampled 30 host trees (height ≥2 m) each in secondary forests, abandoned paddies and formerly mown areas, landslide tracks and riparian forests. Then, we counted the number of larvae following the same method as in 2004 from 19 November

to 1 December 2005. This census could not be done in plantations of C. japonica, because there were no host trees with a height ≥ 2 m. The dbh of the tree investigated in 2 years is up to 62.1 cm. The heights of these host trees were up to 20-25 m.

Number of adults and their behavior

We established a 200-m-long, straight census line inside and at the edge of riparian forests, secondary forests and plantations of *C. japonica*. In the summer season of 2004 and 2005, we recorded the number, behavior type and sex of adults within a range of 5 m above and 5 m across from the investigator along the census lines, except for that inside of plantations of *C. japonica* in 2004. The recording was carried out at 10:00–11:30 on 25 days with fine weather during 27 June–2 August 2004, and at 10:00–11:30 and 16:00–17:30 on 24 fine days during 5 July–8 August 2005. We also recorded the number of males flying consistently around branches of host trees during the period from 15 July–8 August 2005.

Statistical analysis

For each site, the area of breast height was log-transformed; the number of larvae per host tree and adult butterflies per 200 m were log(N + 1)-transformed prior to statistical analysis. We used Tukey-Kramer multiple comparisons to confirm the sites with a significant difference. We used a Pearson correlation (r) between logtransformed data of the area of breast height and number of larvae per host tree at each site and then the significance of the values were tested. We used a chi-square test to compare the number of adults engaging in each type of behavior among the study sites. In the analyses, we treated equal numbers of adults engaging in each type of behavior at each site as the expected value, and tested the differences between the expected and the actual numbers using a chi-square test, i.e., we calculated the expected value by dividing all numbers of adults engaged in each type of behavior by the number of sites.

Results

Distribution and size structure of host trees

Host trees, *C. sinensis* and *C. jessoensis*, having a height of 2 m or more and BA = 19.6 cm² (equivalent to 5 cm in dbh of one stem) or more, were found in secondary forests on gentle slopes, abandoned paddy fields and formerly mown areas, landslide tracks and riparian forest (Fig. 2). In riparian forest, landslide tracks and formerly mown areas, we observed both canopy and small-sized host trees. In the secondary forests, there were more small-sized host trees than at other sites, though not in the canopy layer; small-sized host trees

were only found in the shrub to sub-canopy layers under the canopy of *Q. acutissima* or *Q. serrata*.

The stem densities of C. sinensis and C. jessoensis were lowest in secondary forests and increased in the order of riparian forests, abandoned paddies and formerly mown areas and landslide tracks (Table 1). The densities were significantly biased among the sites. The densities of individuals (clumped stems were regarded as one individual) were also lowest in secondary forests and increased in the order of landslide tracks, riparian forest and abandoned paddies and formerly mown areas (1). The differences among them were significant. Total BA values (cm² ha⁻¹) of C. sinensis and C. jessoensis were lowest in secondary forests and increased in the order of landslide tracks, abandoned paddies and formerly mown areas and riparian forests. The mean BA of individual C. sinensis and C. jessoensis trees was lowest in secondary forests and increased in the order of abandoned paddies and formerly mown areas, landslide tracks and riparian forests with significant differences (Table 1).

Number of larval individuals per host tree

Larvae hardly used any host trees whose height was < 2 m at any of the sites, and there was no difference in the (low) densities of larvae per host sapling (H < 2 m) among the study sites (Table 2). On the other hand, habitats differed in number of larvae found at trees taller than 2 m. The highest numbers occurred in riparian forests, followed by abandoned paddies and formerly mown areas and secondary forests (Table 3). When the value of BA became large, the number of larvae also increased in riparian and secondary forests, but not in abandoned paddies and formerly mown areas (Fig. 3). The pattern was similar in 2005; the number of larvae per host tree and trunk area of host trees researched was highest in riparian forests on sandbanks, followed, in a decreasing order, by landslide tracks, abandoned paddies and formerly mown areas and secondary forests (Table 3). When the value of BA became large, the number of larvae also increased in riparian, landslide track and secondary forests, but not in abandoned paddies and formerly mown areas (Fig. 3).

Adult density and the behavior

In both 2004 and 2005, the observed number of adults was greatest at the edge of riparian forests. The difference in the number of adults between the edge of riparian forests and all the other sites was significant (Table 4). Adults were observed in significantly greater numbers at the edge compared to inside of the riparian forests both in 2004 and 2005. Adults were found also at the edge of plantations of *C. japonica*, but in significantly lower numbers than at the edge of the riparian forests and at the edge of the secondary forests. No adults were observed inside the plantations of *C. japonica* (Table 4).

For males in 2004, puddling behavior was observed most frequently at the edge of riparian forests, but in 2005, it was most frequently observed inside of secondary forests (Fig. 4). For females, 2004 and 2005, puddling behavior was observed most frequently at the edge of riparian forests (Fig. 4). In 2004, at the edge of and inside of the secondary forest and inside of the riparian forest, use of exuding tree sap was observed significantly more frequently than other resources (2004 $\chi^2 = 564.6$, P < 0.001). The same is true at the inside of secondary forest both in 2005 ($\chi^2 = 402.8$, P < 0.001) (Fig. 5). The tree sap of woody species in the secondary forest, Q. acutissima and Q. serrata, was most frequently utilized by S. charonda; inside of the riparian forest, sap of G. japonica and J. mandshurica was utilized. On the other hand, at the edge of riparian forests, puddling behavior was most frequently observed on damp sand at the edge of the river in both 2004 and 2005, and the difference was significant (2004 $\chi^2 = 254.8$, P < 0.001; 2005 $\chi^2 = 644.2$, P < 0.001) (Fig. 5).

In both 2004 and 2005, the roosting behavior was observed significantly more frequently inside secondary forests (Fig. 6). The behavior was significantly biased to females inside secondary forest (2004 $\chi^2 = 12.8$, P < 0.001; 2005, $\chi^2 = 61.7$, P < 0.001). Moreover,

Table 1 Dens	ity (/ha), area	of breast hight (/ha	a) and average area	of breast height of C	. sinensis and C. jessoensis

	Sites					P
	SF^1	APFMA ²	SLT ³	SB ⁴	CP ⁵	
Total area (ha)	1.7	0.63	0.74	0.38	0.98	
Density (no. of stems of host tree/ha)	18.1	119.0	131.1	76.3	0	$\gamma 2 = 440.5, P < 0.001$
Density (no. of host trees/ha)	14.0	98.4	50.0	55.3	0	$\chi^2 = 328.2, P < 0.001$
Total BA (cm ²)/ha	1,800	32,000	17,000	43,000	_	
Maximum BA (m ²)	0.048	0.39	0.34	0.32	_	
Mean BA (m ²)	0.011 ^a	0.031 ^a	0.033^{a}	$0.077^{\rm b}$	-	

All detected host tree were 2 m tall or more and with 50 mm or more of diameter at breast height. Values followed by different letters are significantly different (Tukey–Kramer multiple comparisons, P < 0.05)

¹SF secondary forest, ²APFMA abandoned paddy and formerly mown area, ³SLT site of landslide tracks, ⁴SB sandbank, ⁵CP plantations of Cryptomeria japonica

Table 2 The number of overwintering larvae of Sasakia charonda per host tree whose height were less than 2 m

		SF ¹	APFMA ²	SLT ³	SB ⁴	CP ⁵
2004	No. of trees researched No. of trees where the larvae were observed (%) ⁷	60 (S:9, J:51) ⁶ 1 (1.6%)	60 (S:8, J:52) ⁶ 1 (1.6%)		60 (S:6, J:54) ⁶ 1 (1.6%)	
2005	Mean of the number of larvae per tree No.of trees researched No. of trees where the larvae	0.07 ^a 40 (S:0, J:40) ⁶ 3 (7.5%)	0.05 ^a 40 (S:1, J:39) ⁶ 1 (2.5%)	- 40 (S:1, J:39) ⁶ 2 (5%)	0.02 ^a 40 (S:0, J:40) ⁶ 2 (5%)	- 40 (S:10, J:30) ⁶ 0
	were observed (%) ⁷ Mean of the number of larvae per tree	0.08^{a}	0.03 ^a	0.13 ^a	0.15 ^a	0^{a}

Values followed by different letters are significantly different (Tukey–Kramer multiple comparisons, P < 0.05)

Table 3 The number of overwintering larvae of Sasakia charonda per host tree whose heights were 2 m or more

	SF ¹	APFMA ²	SLT ³	SB ⁴
2004 Number of trees researched No. of trees where the larvae	40 (S 5, J 35) ⁵ 33 (82.5%)	40 (S 16, J 24) ⁵ 39 (97.5%)	_ _	40 (S 11, J 29) ⁵ 40 (100%)
were observed $(\%)^6$ Mean \pm SD of the number of	8.8 ± 14.0^{a}	17.8 ± 16.6^{b}	_	$51.3 \pm 25.3^{\circ}$
larvae per tree Mean ± SD of trunk area of host trees researched	53.4 ± 135.0^{a}	389.3 ± 667.0^{b}	_	$890.4 \;\pm\; 831.0^{\rm c}$
2005 Number of trees researched No. of trees where the larvae were observed (%) ⁶	30 (S 4, J 36) ⁵ 24 (80%)	30 (S 14, J 16) ⁵ 29 (96.7%)	30 (S 1, J 29) ⁵ 27 (90%)	30 (S 11, J 19) ⁵ 29 (96.7%)
Mean ± SD of the number of larvae per tree Mean ± SD of trunk area of host trees researched	7.0 ± 8.2^{a} 135.2 ± 284.9^{a}	$16.9 \pm 14.4^{\rm b}$ $315.0 \pm 285.0^{\rm b}$	$ \begin{array}{r} 18.7 \pm 20.8^{\rm b} \\ 338.5 \pm 667.0^{\rm b} \end{array} $	$40.9 \pm 24.6^{\circ}$ $1120.2 \pm 988.4^{\circ}$

Values followed by different letters are significantly different (Tukey–Kramer multiple comparisons, P < 0.05)

female adults roosting in secondary forests tended to be heavily worn, i.e., of old age.

Egg-laying females and mating couples were only found in and at the edge of riparian forests in both years. When mating couples were observed, the females were very fresh and there were always shells of pupae beside the females. In both 2004 and 2005, the observed numbers of flying adults were greatest at the edge of riparian forests (Fig. 7). At each site, most flying individuals observed were males or individuals of unidentifiable sex. However, the most individuals of unknown sex were probably males, because the size of their wings was smaller than that of the females. The number of individuals chasing other adults of the same species or other organisms was greatest significantly at the edge of riparian forests both in 2004 and 2005. The number of females courted by males was greatest at the edge of riparian forests in both 2004 and 2005 (Table 5). The number of males flying consistently around branches of C. sinensis and C. jessoensis was also significantly larger at the edge of riparian forests than other sites (Table 5).

Discussion

Relationship between natural and artificial disturbances and regeneration of C. sinensis and C. jessoensis

Matsuoka and Sano (2003) reported that overflowing of rivers is one of the factors responsible for regeneration of C. sinensis, and this plant is one of the pioneer tree species forming riparian forests. Our study also supports that C. sinensis is a pioneer tree species strongly depending on a river disturbance and landslides. Some extremely heavy rains cause avalanches, overflows and landslides in this area, since the volcanic deposits prevailing in this area are not very stable. Accordingly, the exposure to mineral soil or new deposits may be required for regeneration of C. sinensis. Although there are few reports on C. jessoensis, we confirmed that this tree species had similar ecological characteristics as C. sinensis.

In the present study, we also showed that the places under the regime of human-made disturbances as well as

¹SF secondary forest, ²APFMA abandoned paddy and formerly mown area, ³SLT site of landslide tracks, ⁴SB sandbank, ⁵CP plantations of Cryptomeria japonica

⁶No. in parentheses shows the number of C. sinensis and C. jessoensis researched. No. of C. sinensis and C. jessoensis represents S and J, respectively

Percentage of numbers of trees where larvae were found to total number of trees investigated

SF secondary forest, ²APFMA abandoned paddy and formerly mown area, ³SLT site of landslide tracks, ⁴SB sandbank

⁵Number in parentheses shows the number of C. sinensis and C. jessoensis researched. S and J represents number of C. sinensis and C. *jessoensis*, respectively ⁶Percentage of numbers of trees, where larvae were found, to total number of trees investigated

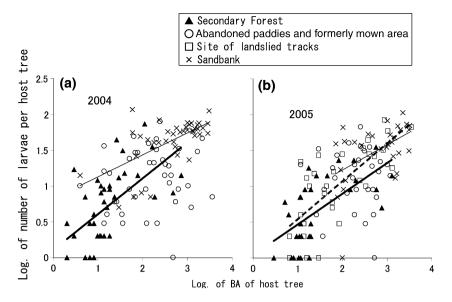


Fig. 3 Relationship between logarithms number (N) of larvae per host tree and basal area (BA) of tree researched at each site. The landslide tracks were only studied in 2005. In 2004, significant positive correlations between the number of larvae per host tree and BA of individual host trees were detected in riparian and secondary forests (secondary forests r = 0.59, thick line, y = 0.50x + 0.11, P < 0.001; riparian forests r = 0.61, thin line, y = 0.31x + 0.82, P < 0.001), but not in abandoned paddies and formerly mown areas

(r = 0.14, P = 0.41). In 2005, significant positive correlations between the number of larvae per host tree and the BA of individual host trees were detected for sandbanks, landslide tracks and secondary forest (secondary forests r = 0.63, thick line, y = 0.43x + 0.04, P < 0.001; landslide tracks r = 0.73, dashed line, y = 0.53x + 0.02, P < 0.001; riparian forests r = 0.50, thin line, y = 0.35x + 0.53, P < 0.01), but not in abandoned paddies and formerly mown areas (r = 0.01, P = 0.96)

Table 4 Average number of adults of Sasakia charonda per 200 m census at each site

	Inside of SF ¹	Edge of SF ¹	Inside of RF ²	Edge of RF ²	Inside of CP ³	Edge of CP ³
2004 2005	$12.9 \pm 14.1^{ac} 4.6 \pm 6.2^{a}$	$15.3 \pm 11.6^{\rm a} \\ 2.6 \pm 2.7^{\rm a}$	$7.2 \pm 9.7^{\rm cd}$ $0.8 \pm 2.0^{\rm be}$	$70.2 \pm 46.3^{\rm b} \\ 24.0 \pm 18.5^{\rm c}$	_ 0	$3.5 \pm 3.0^{\rm cd}$ $0.9 \pm 1.3^{\rm de}$

Values followed by different letters are significantly different (Tukey–Kramer multiple comparisons, P < 0.05) ^{1}SF secondary forest, ^{2}RF riparian forest on sandbank, ^{3}CP plantations of C. japonica

Fig. 4 Number of puddling individuals of males, females and the sum of both sexes. *SF* secondary forest, *RF* riparian forest, *CP* plantations of *C. japonica*



river surroundings are suitable for regeneration of *C. sinensis* and *C. jessoensis*, i.e., it was found that the both tree species are regenerated through clear cutting or log-

ging in the areas of (1) secondary forests and (2) abandoned paddy fields and the surrounding formerly mown areas. This is supported by the observation that, when a

Fig. 5 Number of adults and feeding resources at each site. The proportion of individuals puddling in each food resources is shown as a percentage (%) of the total number of puddling individuals at each site. Food resource items for *Sasakia charonda* in the secondary forests differed from those at the edge of riparian forests. Abbreviations are the same as in Fig. 4

Fig. 6 Numbers of roosting individuals of males, females and sum of both sexes at each site. Abbreviations are the same as in Fig. 4

Fig. 7 Numbers of flying individuals of males, females and unknown sex. Abbreviations are the same as in Fig. 4

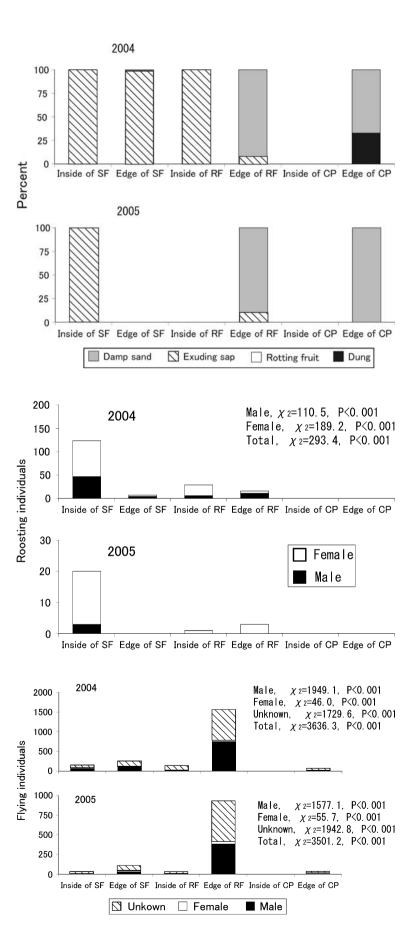


Table 5 Number of chasing adults, female adults courted by males and males flying around branches of C. sinensis and C. jessoensis persistently

Year		Inside of SF ¹	Edge of SF ¹	Inside of RF ²	Edge of RF ²	Inside of CP ³	Edge of CP ³	P
2004	Chasing behavior	20	48	30	505	_	13	$\chi^2 = 1484.6, P < 0.001$
	Female adults courted by males	7	4	0	14	_	0	
2005	Chasing behavior	2	16	7	225	0	3	$\chi^2 = 955.1, P < 0.001$
	Female adults courted by males	0	0	0	8	0	0	,
	Males flying around branches consistently	0	2	8	49	0	0	$\chi^2 = 192.1, P < 0.001$

¹SF secondary forest, ²RF riparian forest on sandbank, ³CP plantations of C. japonica

secondary forest stand is logged, *C. sinensis* germinates at the edges of clearings (Kobayashi et al. 2004).

Importance of riparian forests and secondary forests to *S. charonda* populations

Our results suggested that riparian forests and secondary forests played important, but different roles in maintenance of S. charonda populations, i.e., the overwintering larval density was higher in riparian forests than at other sites, probably due to its presence of large host trees. The number of adults observed was greatest at the edge of riparian forests, and a wide variety of adult behaviors was observed in and around there. On the other hand, male and female adults used secondary forests as well as feeding and roosting sites, respectively. Consequently, it was suggested that riparian forests function as suitable habitats for the larvae and for adult puddling, mating and breeding behaviors, and secondary forests as suitable habitats for adult feeding and roosting behaviors. Probably, the relatively high densities of S. charonda populations in this area are guaranteed by the presence of habitats with both secondary and riparian forests.

In addition, larval density was relatively high at landslide tracks, as well as in riparian forests, suggesting that the role of landslide tracks in *S. charonda* populations is similar to that of riparian forests on sandbanks. Probably, the landslide tracks can function as a source of supply of host trees to riparian forests, when those on sandbanks are disturbed by overflowing of rivers. However, further studies are needed to clarify this possibility.

Patterns in the behavior of S. charonda

Our findings suggest that adults of *S. charonda* utilize the edges of streams for puddling. It is well known that adult Lepidoptera belonging to many families feed from damp sand at edges of streams (Norris 1936; Pivnick and McNeil 1987).

It is likely that the edges of riparian forests, where the number of *S. charonda* males were greatest, functioned as mating sites, as mating and laying eggs by females was restricted to this habitat (Table 5). Thus, the males

flying around branches of *C. sinensis* and *C. jessoensis* at the edge of riparian forests (Table 5) were probably searching for freshly emerged females.

We suggested that virgin females of *S. charonda* mate soon after emergence and lay eggs at the edge of riparian forests. Afterwards, they may lose their body weight and disperse into secondary forests and roost there to avoid persistent courting by males. Baguette and Nève (1994) reported that the female adults of *Proclossiana eunomia* mate just after emergence, lay eggs near the mating sites, and after getting rid of some body weight, disperse away from their emergence sites.

Conservation implications

Our results suggest that both riparian and secondary forests form necessary components of the habitats for *S. charonda* populations. To maintain the riparian forests where *C. sinensis* and *C. jessoensis* regenerate, it is necessary to maintain sufficient width of the disturbed riparian areas as sites for regeneration of *Celtis* species. This may include halting construction barriers to prevent landslides and shore concrete embankments. A sufficient width of a riverbank with minimum barriers promotes the formation of sandbanks through floods. Rivers with no or few concrete embankments provide adults of *S. charonda* with damp sands at the edges of streams for puddling.

In addition, it is also important to ensure secondary forests containing Q. acutissima or Q. serrata, as discussed. Kobayashi et al. (2004) studied the maintenance mechanism of S. charonda populations in agroecosystems where only secondary forests were present in the habitat of this species. They showed that partial deforestation of secondary forests containing C. sinensis trees and stands of *Q. acutissima* with the alteration in traditional land use leads to an increase in the density of the host trees through the formation of new forest edges where the host trees can regenerate and grow, but to a decrease in the densities of both adults and overwintering larvae of S. charonda. Thus, the habitat requirements of S. charonda and its host trees differed more or less from each other. To cover these different habitat requirements in the butterfly and its host trees, it is necessary to continuously create new forest edges in the habitat without decreasing the total area of secondary forests. Traditional coppicing management is a highly recommended practice for creating such habitat conditions in the habitat consisting of only secondary forest (Kobayashi et al. 2004). In Europe, it is also reported that the critically endangered woodland butterfly, Euphydryas maturna, depends on successional woodland stages with young trees, either in coppiced woodland or at clearings (e.g., Konvicka et al. 2005; Freese et al. 2006). On the other hand, in landscapes consisting of riparian and secondary forests, traditional coppicing management is not necessarily needed in secondary forests, because the secondary forests played an important role for adult males to puddle exuding tree sap of Q. acutissima or Q. serrata and for females to roost on the tree trunks. If the establishment of barriers to prevent landslides and concrete bank embankments are unavoidable for other reasons, the importance of secondary forests will increase as a means to ensure the existence of refuges. In such cases, it is necessary to periodically conduct coppice management in riparian forests downstream from barriers and dams to promote the regeneration of the two host trees, C. sinensis and C. jezoensis.

We also recommend that secondary forests not be converted to coniferous forests, such as plantations of *C. japonica*, because such plantations are completely unsuitable for the butterfly.

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