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2 Population stability and asymmetric migration of caddisfly populations, *Stenopsyche marmorata*
3 (Stenopsychidae), in a forest-agriculture landscape.

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Abstract

In river systems, frequent floods generally decrease the abundance of riverine species, and recent studies have reported that the degree of flood disturbance changes along agricultural gradients. However, the interactive impacts between anthropogenic and flood disturbances on migration dynamics are not well tested. In a forest-agricultural landscape in northern Japan, we observed the population stability (fluctuations in abundances) and migration dynamics (directional gene flow) of a net-spinning caddisfly, *Stenopsyche marmorata* (Stenopsychidae), throughout the snowmelt flood period to test whether 1) population stability decreases along agricultural gradients, 2) asymmetric migration occurs from stable populations in forested streams to unstable populations in agriculturally altered streams, and 3) genetic diversity is higher in stable populations. The abundance of *S. marmorata* was related to agricultural development (i.e., pasture cover in catchments); its abundance was higher in agricultural streams before the flood (March), but the quantitative relationship was inverted just after the flood (May) and recovered six months post-flood (November). The resistance index (post-flood abundance divided by pre-flood abundance) showed a negative correlation with pasture cover in the catchment, indicating that population stability decreases along agricultural gradients. The long-term effective number of migrants (N_{em}) and recent migrants (assignment tests) estimated from the genetic analysis showed asymmetric colonization from stable populations in forested sites to unstable populations in agricultural sites. In contrast, genetic diversity was not related to agricultural development, but private allelic richness

(number of unique alleles) was higher in forested streams than in agricultural streams. Our findings suggest that forested streams serve as sources for unstable populations in agriculturally impacted streams and contribute to high genetic diversity at a catchment scale.

Keywords

snowmelt flood, landscape genetics, meta-population, disturbance, anthropogenic impacts

Statements and Declarations

Conflict of interest: The authors declare no competing interests.

48 **Introduction**

49 Immigration and emigration among local populations are key components in meta-population
50 dynamics and contribute to the regional persistence of species (Hanski and Thomas 1994; Hanski 1998).
51 Source–sink relationships are one of the general forms of a meta-population structure, where a source
52 population represents a migration source to other local populations (i.e., net exporter of individuals), and
53 a sink population represents a migration sink from the source population (i.e., net importer of individuals)
54 (Pulliam 1988; Pulliam and Danielson 1991). Source populations are more likely to occur in stable and
55 growing populations than in decreasing populations because the former represents good reproduction and
56 survival and can potentially become substantial emigration sources. Generally, most populations are
57 temporally unstable with a large fluctuation of individuals; nevertheless, these populations can persist in
58 focal habitats by continued immigration from source populations (Pulliam 1988, Dias 1996). Therefore,
59 detecting and sustaining source habitats (populations) are essential to maintain the entire meta-population
60 structure and are typically considered priority areas for species conservation.

61 Flood disturbance is the major determinant of population fluctuations in instream organisms,
62 and severe floods often cause a catastrophic decrease in local populations (Fisher et al. 1982). The effect
63 of flooding is dependent on the availability of instream flow refugia (Townsend and Hildrew 1994;
64 Townsend et al. 1997). Flow refugia, defined as stable habitats with low hydraulic stress during a flood
65 (Lancaster and Hildrew 1993), are generally created more in heterogeneous channels (e.g., large boulders,
66 woody debris, backwaters and inundated floodplains) (Sedell et al. 1990), and organisms inhabiting

heterogeneous channels show high resistance and resilience to flood disturbance (Palmer et al. 1996; Matthaei et al. 2000; Sueyoshi et al. 2014). These resilient channels or habitats that can be sources of migrants for disturbed habitats after flooding are distributed across river networks, thereby shaping the source–sink dynamics of meta-populations at a catchment scale (Lancaster and Belyea 1997; Lancaster 2000).

Recently, many studies have reported the negative consequences of instream habitat homogenization caused by various types of anthropogenic impacts, such as land use, water degradation and fine sediment deposition (Larsen et al. 2009; Maloney et al. 2011; Bini et al. 2014). Such habitat homogenization not only reduced biotic and abiotic diversities at base flows but also reduced the resistance of riverine organisms to flood disturbances due to the loss of flow refugia (e.g., Parkyn and Collier 2004; Mesa 2010). For example, channelization restricted floodplain areas and diminished backwaters that function as useful flow refugia during flooding (Negishi et al. 2002). If the source habitats in river networks are degraded by such artificial factors, metapopulations depending on the source–sink dynamics cannot be maintained (Vuilleumier and Possingham 2006). However, the impacts of flooding on the migration dynamics of riverine organisms along gradients of anthropogenic disturbances are not well known.

We previously examined aquatic insects' resistance (i.e., survival rates) to an annual snow-melt flood disturbance in a forest-agriculture landscape. In a previous study, we revealed that most species

were significantly decreased by flooding in agriculturally impacted streams compared to forested streams in northern Japan (Sueyoshi et al. 2017). Eventually, approximately 50 % of taxa were eliminated from the site with the highest land use intensity. In the study catchments, agriculturally impacted streams were characterized by low environmental heterogeneity and much fine sediments, reducing the availability of refugia and easily washing out organisms living in the substrate. A net-spinning caddisfly, *Stenopsyche marmorata* (Stenopsychidae), the dominant species widely distributed across forest-agricultural streams, was affected most severely by the interacting impacts. The species is highly resilient to flood disturbance because its nets tightly connect stones and strengthen substrate stability (Takao et al. 2006). Nevertheless, the density declined to almost zero in the agricultural streams throughout the flooding season. Because the snowmelt flood season precedes the reproductive season (i.e., emergence period) of *S. marmorata*, the recovery of populations that decreased severely by flooding may depend on immigration from surrounding stable populations. Therefore, *S. marmorata* populations are suitable for testing the effects of population instability on migration dynamics in forest-agricultural landscapes.

In this study, to elucidate the impacts of flooding on migration patterns in human-modified landscapes, we observed the subsequent population dynamics after flood disturbance (i.e., recovery) and the genetic structure of *S. marmorata*. We estimated the migration dynamics among populations using gene flows because genetic data provide useful information to estimate the movement of individuals (Slatkin 1987; Storfer et al. 2007), and recent analyses enable the estimation of asymmetric migrations at

fine spatial scales (Beerli and Felsenstein 1999, 2001; Piry et al. 2004). We hypothesized that (1) gene flows between stable (forested sites) and unstable populations (agriculturally impacted sites) are asymmetric and higher from stable to unstable populations than in the opposite direction and (2) the stable populations show higher genetic diversity compared to unstable populations because populations experiencing bottlenecks often reduce genetic diversity (e.g., Nei et al. 1975; Leberg 1992; Spencer et al. 2000).

Methods

Study sites

The study sites were in the Kitamihorobetsu River, Hokkaido, a subarctic region of Japan. The catchment area of the Kitamihorobetsu River is 416 km² and is covered by forests (78 %), natural grasslands (6 %), pastures (15 %) and other land uses (1 %). Many small patches of pastures are located along the mainstream and tributaries of the Kitamihorobetsu River (Fig. 1). This river is in a subarctic region with heavy snowfall in winter, which causes large snowmelt floods in the early spring season, usually from early April to late May, for approximately two months (Table 1, Appendix Fig. S1). We selected 27 sites for observations of population dynamics and six sites for observations of the migration dynamics of *S. marmorata* in three tributaries of the Kitamihorobetsu catchment (Kitamihorobetsu, Penkenai and Ketobetsu streams) (Fig. 1).

We calculated the percentage of pasture cover within each catchment area as an indicator of agricultural impacts (% pasture) because this index is strongly correlated with the habitat modification of stream environments associated with agricultural activity in the studied catchments (e.g., sedimentation of fine sediments, water degradation and homogenization of channel hydromorphology; Sueyoshi et al. 2016). The range of pasture cover in our study catchments was relatively small, less than 18 %; however, land development was concentrated along the stream channels, and clear-cutting of riparian forests increased the inputs of fine sediments in agricultural streams (Appendix Fig. S1). The % pasture was calculated based on an available vegetation/land-use map (scale of 1:50,000, Ministry of the Environment of Japan, 1998) using a function of Spatial Analyst in ArcGIS 10.0 (ESRI, USA) and ranged from 0-17.9 % in our study sites. Six sites included in the genetic analysis exhibited three levels of agricultural development in the range of our study catchments: two upstream sites in the Kitamihorobetsu and Penkenai streams were characterized by low (0 % and 1.0 %) agricultural development; two downstream sites in the Penkenai and Ketobetsu streams were characterized by moderate (11.7 % and 10.2 %, respectively) agricultural development; and one downstream site in the Kitamihorobetsu stream and one upstream site in the Ketobetsu stream were characterized by high (both 17.9 %) agricultural development (Fig. 1).

Ecological characteristics of *S. marmorata*

The target species of this study is a net-spinning caddisfly, *S. marmorata* (Stenopsychidae,

Trichoptera). We chose the following selection criteria: 1) general species distributed across forest-agricultural landscapes; 2) high fluctuations in abundance throughout the snowmelt flooding period (Sueyoshi et al. 2017); 3) well-understood phylogeography (Saito et al. 2018); 4) microsatellite markers that can estimate fine-scale genetic structures and gene flows (Yaegashi et al. 2014); and 5) well-established detailed ecological traits and life cycles (Gose 1970). This species prefers rocky substrates and shows high resistance to flood disturbance because the net connects the stones and increases bed stability (Takao et al. 2006; Nunokawa et al. 2008). Movements of larvae (especially for later instars) are limited because of their coherent nets, whereas the dispersal distance of adult flies is very long (estimation based on observed data, 2.5-12 km in Nishimura 1981; genetic data, 12-18 km in Yaegashi et al. 2014). Therefore, most of the movement of individuals between local populations would occur in the emergence period. The emergence period is once from May to July after the snowmelt flood season in a subarctic region (*S. griseipennis*, a synonym of *S. marmorata*, in Gose 1970).

Sampling design

At each of the 27 sites, we first collected quantitative samples of larvae of *S. marmorata* using twelve quadrats (25*25 cm) with a Surber net (0.3 mm mesh) before (March) and after the snowmelt flood (May) in 2011 to evaluate the effects of flood disturbance on *S. marmorata* populations. We set two quadrats on each of the six transects across the reach during the study period. These two samplings (March and May) were conducted to collect individuals from various mesohabitats to examine the effects of

flooding on all insect species (see details in Sueyoshi et al. 2017). *S. marmorata*, the study species in this study, was mainly found in riffle habitats; therefore, we focused on riffle habitats to examine the re-establishment of populations of *S. marmorata* after the flood. Three kick samples (1 kick sample collected over 2 min in a 1 m² area) were collected using a D-frame net (1 mm mesh) after the emergence period (November 2011) (Gose 1970; Table 1). Kick sampling in riffles could more efficiently collect individuals of the species than quadrat sampling across the reach.

Data analysis

To clarify the distribution (i.e., population density) of *S. marmorata* in agricultural gradients and the impacts of a flood on each population, we constructed generalized linear models (GLMs) with Poisson error distributions for each of the three observation periods (March, May and November). We did not use density per area (ind. m⁻²), and instead used the total number of individuals collected at twelve quadrats or three kick samples as a response variable because the count data are generally better fitted using Poisson than Gaussian distributions used for continuous variables in GLM (Qian 2017). Thus, the response variable was the total abundance at each site, and the explanatory variable was % pasture. Additionally, the resistance index to flood disturbances was calculated using the first two samples (March and May) collected by the same sampling methods (Sueyoshi et al. 2017). The index was calculated by the post-flood abundance divided by the pre-flood abundance. Higher resistance represents higher stability of the population density between pre- and post-flood. To examine the relationships between the

resistance index and % pasture, a GLM with a Gaussian error distribution was performed. The significance of the coefficients of an explanatory variable was judged by the Akaike information criterion (AIC). If the ΔAIC (difference between the full and null models) was larger than 2, the explanatory variable was influential for the response variable (Burnham and Anderson 2002). All statistical analyses were conducted using the R environment for statistical computing (R Core Team 2022) with the package MuMIn (Barton 2022).

Sampling and genetic microsatellite genotyping

For the genetic analysis, we collected 23-32 individual *S. marmorata* larvae from each of six sites (KiU, KiD, KeU, KeD, PeU and PeD) in November 2011 (Table 1; Fig. 1). These sites were selected based on the results of the first two sampling periods (March and May in Fig. 2), with different combinations of population stability, agricultural impacts, and longitudinal location (i.e., up- and downstream). The specimens were preserved in 100 % EtOH. A total of 163 individuals were genotyped (Table 3). Total genomic DNA was extracted from the ethanol-preserved tissue of the specimens and purified using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA). Seven microsatellite loci (Steno01,03, 04, 07, 08, 09, and 10) developed for *S. marmorata* (Molecular Ecology Resources Primer Development Consortium 2009) were amplified by polymerase chain reaction (PCR). These markers can be used to assess fine-scale gene flows within a geographic distance of 40 km (Yaegashi et al. 2014), and previous studies have shown asymmetric migrations in stream networks using fewer than ten markers

(Yamazaki et al. 2011; Kanno et al. 2014). Each 10- μ L reaction volume contained 10 ng template DNA, 0.25 U rTaq polymerase (Toyobo, Osaka), varying concentrations of primers, 1.2 μ L of 25 mM $MgCl_2$, 2.0 μ L of 2 mM dNTP mix, and 2.0 μ L of 10 $\times$ rTaq polymerase buffer. The PCR protocol was as follows: 95°C for 2 min; 35 $\times$ (95°C for 30 s, 47 or 50°C for 30 s, 72°C for 1 min); and a final extension step of 72°C for 5 min. We analysed the obtained fragment sizes on an ABI 3130xl automated sequencer (Applied Biosystems) with a GeneScan 500 LIZ size standard (Applied Biosystems), and the size of each peak was determined using Peak Scanner 1.0 (Applied Biosystems).

Genetic diversity

We calculated the expected heterozygosity (H_e) and fixation index (F_{is}) for each population using GENALEX 6.4 (Peakall and Smouse 2006), and rarefied allelic richness and rarefied private allelic richness (unique alleles that appeared only in one population) were calculated using HP-Rare v. June-6-2006 (Kalinowski 2005). We checked the evidence of null alleles using MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004) and tested the linkage disequilibrium and deviation from Hardy–Weinberg equilibrium for each population and locus using GENEPOP 4.2 (Raymond and Rousset 1995). Significant levels were adjusted by Bonferroni correction. To test the relationships between agricultural development and each genetic diversity, we checked their correlations by using GLMs with Gaussian error distributions. The significance of the coefficients of an explanatory variable was judged by the Akaike information criterion (AIC).

Genetic clustering, estimation of migration rates, and assignment tests

First, we estimated the average migration rates among local populations using a coalescent-based approach implemented in MIGRATE-N3.6.4 (Beerli and Felsenstein 1999, 2001). The method uses Bayesian inference to estimate the pairwise mutation-scaled migration rate, M ($M = m/\mu$, where m is the migration rate per generation and μ is the mutation rate per generation), and mutation-scaled effective population size, θ ($\theta = 4N_e\mu$, where N_e is the effective population size) (Beerli 2006). This method allows the estimation of asymmetrical gene flow among populations and is therefore appropriate for clarifying migrations among populations with differences in instability. Although MIGRATE-N was often used to estimate long-term gene flows (generally across $4N_e$ generations), a recent study reported that the estimation was influenced by the current migration change and provided better estimates of the recent migration rate than the other disequilibrium-based method (Samarasin et al., 2017). Therefore, we used this estimation for migration dynamics in our study regions. We clustered all populations based on genetic distance using POPTREE2 (Takezaki et al. 2010) prior to the estimation of gene flow. The D_{sw} distance (Shriver et al. 1995), which can be used for microsatellite repeats, was used for clustering via the unweighted pair group method with arithmetic mean (UPGMA). Then, we estimated the migration rates among clustered groups by using MIGRATE-N. Additionally, we estimated the migration rates between upstream and downstream areas in each of the three streams because these two areas of each stream belonged to different genetic clusters (see Results) and showed different combinations of agricultural

development: low vs. high in the Kitamihorobetsu stream, low vs. moderate in the Penkenai stream and high vs. moderate in the Ketobetsu stream (Fig. 1, Table 3).

We ran Markov chain Monte Carlo runs with 100 sampling increments, 350,000 recorded steps and 30,000 burn-in steps using the Brownian motion model with static heating of 4 temperatures (1.0, 1.5, 3.0, and 1000000.0). The prior distributions of M and θ were set to include the upper limit of the posterior distributions as an exponential prior distribution. The average effective number of migrants between populations per generation (N_{em}) was calculated as $M \times \theta / 4$. By referring to Ishiyama et al. (2015), we also calculated net immigration (the total number of effective immigrants minus the total number of effective emigrants) for each of the six populations and genetic clusters. A negative value of N_{em} indicates that the number of emigrants exceeds the number of immigrants.

We also employed the assignment test based on the Bayesian method by Rannala and Mountaion (1997) implemented in Geneclass 2.0 (Piry et al. 2004) to assess some recently observed migrations and determine the most likely populations of origin for each case. This test computed the probability of a particular multilocus genotype of each individual to be encountered in a given population within a few generations. The probability was calculated using the method of Paetkau et al. (2004) based on 10,000 Monte Carlo simulations and a type I error rate of 0.01. Assignment tests were conducted among three genetic clusters and six original populations. We determined the source of each individual as being the population having the highest probability.

Results

Local population dynamics of *S. marmorata* along agricultural gradients

The population density of *S. marmorata* ranged from 0 to 92 ind. m⁻². *S. marmorata* was never found at three sites in the upstream region of the Ketobetsu stream on all sampling occasions (Fig. 1). These three sites were excluded from the statistical analyses. In GLM analyses, Δ AIC between the full and null models was larger than 2 for all response variables (Table 2), suggesting that % pasture was influential for all response variables. The abundance of *S. marmorata* exhibited a positive correlation with pasture cover before the flood (Mar) but a negative correlation after the flood (May). The relationship at six months after the flood (Nov) was positive (Fig. 2). The populations at both KiD and KeU, which represented the highest pasture cover, decreased from 10.7 ind. m⁻² (Mar) to 0 (May) but recovered to 12.7 and 6.0 ind. m⁻² (Nov), respectively. The resistance index showed a positive correlation with pasture cover. Among the six sites included in the genetic analysis, the populations at sites with low and moderate pasture cover (KiU, PeU, PeD and KeD) were relatively stable during the year, whereas those at sites with high pasture cover (KiD and KeU) were unstable and showed high fluctuations in population densities.

Genetic diversity

There was no evidence of null alleles among all loci in all populations. Significant linkage disequilibrium was detected only in the BD population at the combined Steno02 and 06 loci (corrected $P < 0.05$). Significant deviation from Hardy–Weinberg equilibrium was detected only in the BD population

at Steno 07 (corrected $P < 0.05$). However, other populations showed nonsignificant linkage disequilibrium and deviation from Hardy–Weinberg equilibrium at all loci. We therefore did not exclude these loci from any analysis. Seven microsatellite loci were polymorphic (the number of alleles ranged from 6–11). Similar values of genetic diversity (A_r and H_e), except for P_r , were obtained among the six populations (Table 3), and genetic diversity presented a nonsignificant correlation with agricultural development (ΔAIC between the full and null models < 2 ; Table 2, Appendix Fig. S2). In contrast, private allelic richness (P_r) showed a negative correlation with agricultural development (ΔAIC between the full and null models = 8.46; Table 2, Appendix Fig. S2).

Genetic clustering

The six populations were clustered into three groups: cluster 1 (KiU, PeU), cluster 2 (KiD, PeD, KeD) and cluster 3 (KeU), which were supported by high bootstrap values (Fig. 3). This clustering reflected agricultural development and positions in the stream network. Cluster 1 (KiU, PeU) consisted of upstream sites with low agricultural development, cluster 2 (KiD, PeD, KeD) consisted of downstream sites with moderate or high agricultural development, and cluster 3 (KeU) consisted of an upstream site with high agricultural development (Figs. 1, 4).

Asymmetric migration

Recent migration among the six populations estimated by the assignment test showed that self-assignment (where the assigned population was the sampled population) was relatively high in an

upstream site of the Kitamihorobetsu stream (KiU), up- and downstream sites of the Penkenai stream (PeU, PeD), more than 30 %, whereas low in the other three sites (KiD, KeD, KeU), less than 20 %. The origin of all sampled individuals was biased towards the Penkenai River (PeU, PeD) (Table 4). Recent migration of the three genetic clusters also showed similar patterns; the percentage of assigned individuals was the highest in cluster 1 (KiU, PeU) or cluster 2 (KiD, KeD, PeD) and the lowest in cluster 3 (KeU) for all sampled clusters (Table 4).

We estimated long-term migration rates among the three genetic clusters and between the up- and downstream sites within each stream. The up- and downstream sites within each stream belonged to different genetic clusters and showed different combinations of agricultural development. The cluster setting enabled us to separately examine the effects of agricultural development (i.e., population stability) and flow direction (i.e., up- and downstream gradients) on migration.

All estimated θ and M values for the three clusters significantly differed from zero (95 % confidence intervals did not overlap zero). Estimated effective migration sizes ($N_e m$) among three genetic clusters showed asymmetric migration, and the values were higher for migrations from cluster 1 (KiU, PeU) to clusters 2 (KiD, PeD, KeD) and 3 (KeU) and from cluster 2 (KiD, PeD, KeD) to cluster 3 (KeU) (Fig. 4; Appendix Table S1). Specifically, $N_e m$ from cluster 3 (KeU) to the other clusters was less than half of $N_e m$ from clusters 1 and 2. The results regarding net immigration showed that cluster 1 and cluster 2 served as net migration sources (negative net immigration), whereas cluster 3 served as a net migration

sink (positive net immigration) (lower part of Appendix Table S1).

Significant asymmetric migration was found between the upstream and downstream parts of each of the three streams (Fig. 5; Appendix Table S2). In the Kitamihorobetsu stream, a higher N_{em} of downstream migration and negative net immigration in an upstream population indicated that an upstream population served as a source for a downstream population. In contrast, in the Penkenai and Ketobetsu streams, the higher N_{em} of upstream migration and negative net immigration in downstream populations indicated that downstream populations served as sources for upstream populations. The results for the Kitamihorobetsu and Ketobetsu streams showed that sites with low and moderate agricultural development (i.e., stable populations) provided individuals to sites with high agricultural development (i.e., unstable populations), whereas the Penkenai stream showed asymmetric migration from sites with moderate agricultural development to sites with low agricultural development.

Discussion

Flow directions or environmental gradients along river networks often shape the asymmetric migration dynamics of stream organisms (e.g., Kanno et al. 2011; Terui et al. 2014; Nakajima et al. 2021). In this study, recent and long-term asymmetric migrations of *S. marmorata* populations were found across the catchment; however, the migratory directions observed were different within and between each of the three tributaries. The decreasing population stability along agricultural gradients and different land uses in

each tributary could be the reason why migratory directions were biased. Previous studies have reported that flooding frequently induces asymmetric migration through the creation of population stability heterogeneity (e.g., Johnson 2004; Shama et al. 2011; Chiu et al. 2023). Our findings indicate that, beyond the impacts of flooding, artificial land use within catchments can further modify the migration dynamics by increasing the vulnerability of instream organisms to flood disturbances. Although we focused on only *S. marmorata*, the interactive impacts between natural and anthropogenic disturbances on migration dynamics are also highly likely to be observable in other species and ecosystems because environmental stochasticity is a proxy of the migration dynamics of metapopulations (Hanski 1998).

S. marmorata was more abundant in agriculturally impacted streams before the flood (Mar) and in forested streams just after the flood (May). These patterns and the negative relationship between the resistance index and % pasture indicated that the populations of *S. marmorata* were more stable in forested streams. While the species can show high resistance to flood disturbances in rocky substrates because of their strong silky nets (Takao et al. 2006), clearcutting along the channels and agricultural land use in the catchments can enhance sediment inputs into streams (Sweeney & Newbold 2014; Appendix Fig. S1) and may increase the mobility of substrate materials and living individuals during flood events. The population densities decreased by flood disturbance partially recovered and showed a positive relationship with agricultural gradients in November. Although the sampling method employed in the period differed from that in previous periods (see details in Methods), the shift from a negative correlation in May to a positive

correlation in November suggests the recovery of local populations in agricultural streams throughout the emergence and oviposition periods. Thus, stability in populations of *S. marmorata* was higher in forested streams than in agricultural streams.

We hypothesized that *S. marmorata* showed asymmetric migration in the river networks and that directional migration occurred from stable populations at forested sites to unstable populations at agriculturally impacted sites. Both recent (assignment tests) and long-term migrations (*Nem*) showed similar migratory dynamics; more individuals colonized from stable to unstable populations than in the opposite direction. Specifically, both estimations of recent migrations among all six populations and three clusters resulted in zero assignments to cluster 3, suggesting that the most unstable population upstream of the Ketobetsu River was dependent on colonization from surrounding populations and became the almost complete sink of individuals. Long-term and recent migration dynamics often show different patterns in river networks (e.g., Yamazaki et al. 2011; Ishiyama et al. 2015). Similar recent and long-term migration dynamics in our study river could be due to the predictable and annual disturbances by the interaction between snowmelt flooding and long-term press disturbance over 100 years by agricultural development. The interactive impacts have gradually degraded the populations in agriculturally impacted streams from a long-term perspective, formed asymmetric migrations along the gradient of population stability, and resulted in the current strong source–sink populations.

However, some combinations of local populations showed the reverse direction of migration,

from unstable to stable populations (higher assignments to the downstream population of the Penkenai River and upstream migration in the Penkenai River in long-term migration). There are two possible causes for this pattern in the studied rivers. First, the general dispersion of *S. marmorata* is highly biased in the upstream direction. Nishimura (1981) reported that the upstream dispersal of adult flies was approximately 3 times higher than their downstream dispersal; therefore, migrants from downstream to upstream populations should be more abundant in natural rivers. Second, moderately stable populations (KeD and PeD) at downstream sites showed a comparable individual density to stable populations at forested upstream sites (KiU and PeU) after the flood. The surviving individuals can contribute to reproduction and dispersal to surrounding populations. Thus, asymmetric migration occurred from moderately unstable populations to stable populations. In contrast, the observation of downstream-biased migration in the Kitamihorobetsu River and overland migration from cluster 1 to cluster 3 supported our hypothesis. The migration patterns recorded in the Kitamihorobetsu River provide particularly strong supportive evidence because migrants from upstream to downstream sites were more abundant, although the general dispersal pattern of *S. marmorata* is upstream biased. Migrants across different streams were also identified. The geographical distances between genetic clusters or up- and downstream sites within each stream ranged from approximately 4 to 12 km. *S. marmorata* can fly up to 12 km overland and 18 km along the riverline (estimates based on observed data, 2.5-12 km in Nishimura 1981; and genetic data, 12-18 km in Yaegashi et al. 2014). Therefore, individuals could be supplied to unstable populations across different streams. These

results suggested that upstream-biased asymmetric migration in natural systems can be altered by habitat changes resulting from agricultural land use, but stable populations in forested streams can supply individuals and sustain subpopulations in agriculturally impacted streams.

We hypothesized that genetic diversity (heterozygosity and allelic richness) would be higher in more stable populations. However, genetic diversity (He and allelic richness) showed no correlation with the level of agricultural development and presented relatively high values at all sites. Genetic diversity in unstable populations depends on the dispersal ability, number of populations and reproductive system of the species involved (Berendonk et al. 2009; Ray 2001). Berendonk et al. (2009) compared stable populations of three midge species to unstable populations of three different midge species and reported low genetic diversity in unstable populations. In this case, the unstable populations were not near source populations; therefore, recovery depended on self-recruitment (i.e., high inbreeding coefficients were observed), and the opportunity for genetic drift increased. In our study catchment, source populations were distributed along the river, and individuals frequently migrated among populations. Therefore, sink populations could receive immigrants from various sources and maintain high genetic diversity despite annual bottlenecks caused by snowmelt floods. In contrast, private allelic richness (i.e., the number of unique alleles) showed a negative relationship with agricultural development, which indicated that gene alleles present in unstable populations with high agricultural development became subsets of the alleles of stable populations. To maintain regional genetic diversity, population sources with more private alleles

should be preferentially preserved.

Instream organisms adapt to seasonal natural disturbance regimes and maintain populations (Lytle and Poff 2004); however, human impacts have drastically altered disturbance regimes and changed metapopulation dynamics (Zeigler et al. 2017). If the altered disturbance regime exceeds the recovery capacity of the metapopulation, the species will be extirpated from the system. Under the current land use, having a low proportion of artificially altered areas in the studied catchment, the metapopulations can be maintained despite annual snowmelt floods. However, future global climate change may increase the intensity and frequency of hydrological disturbances (Hirabayashi et al. 2013; Milly et al. 2002). Therefore, we should carefully observe the population dynamics in forest-agricultural landscapes and need to predict metapopulation dynamics under changing climate scenarios.

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Author Contributions

All authors discussed the study plan. M.S. and N.I. conducted the observation and collected

samples. M.S. and K.T. did the genetic analyses. All authors contributed critically to the draft and gave final approval for publication.

Data accessibility

Data available from the figshare repository [https://doi.org/10.6084/m9.figshare.14333204.v](https://doi.org/10.6084/m9.figshare.14333204.v1)

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Declaration of competing interest

All authors have no conflict in interest.

Supporting Information

Supporting Information can be found online in the Supporting Information section.

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592 Tables

593 Table 1

594 Sampling times, snowmelt flooding period and emergence period of *Stenopsyche marmorata* in 2011.

595 Detailed sampling information is provided in the Methods section. The emergence period in Hokkaido

596 refers to Gose (1970).

2011	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Sampling for population dynamics			12 quad rats		12 quad rats						3 kick samples	
Sampling for genetic analysis											23-32 ind.	
Snowmelt flood												
Emergence period of <i>S. marmorata</i>												

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598

Table 2. Summary of results of GLM for abundances in each sampling period, resistance index, and genetic diversities (allelic richness, expected heterozygosity and private allelic richness). The full model with $\Delta AIC > 2$ compared to the null model is represented in bold.

Variable	Model	Intercept	coefficients of %pasture	logLik	AIC	ΔAIC
Abundance (Mar)	full	2.55	0.034	-158.96	321.9	0.0
	null	2.85		-167.85	337.7	15.8
Abundance (May)	full	2.56	-0.078	-83.59	171.2	0.0
	null	2.03		-103.24	208.5	37.3
Abundance (Nov)	full	3.23	0.020	-101.18	206.4	0.0
	null	3.40		-106.68	215.4	9.0
Resistance	full	1.24	-0.074	-17.37	41.9	0.0
	null	0.63		-24.57	53.7	11.8
<i>Ar</i>	full	6.24	-0.043	-3.98	14.0	0.0
	null	5.82		-5.04	14.1	0.1
<i>He</i>	full	0.69	-0.003	13.50	-21.0	0.0
	null	0.67		12.05	-20.1	0.9
<i>Pr</i>	full	0.51	-0.018	8.28	-10.6	0.0
	null	0.33		3.05	-2.1	8.5

604 Table 3

605 Agricultural development and genotype data of six populations. % Pasture, pasture cover within a

606 catchment area; N, number of samples subjected to genotyping; H_e , expected heterozygosity; F_{is} , fixation

607 index; Ar , allelic richness; Pr , private allelic richness.

Site	% Pasture	N	H_e	F_{is}	Ar	Pr
KiU	0	32	0.68	-0.10	5.97	0.44
PeU	1.0	30	0.69	-0.02	6.17	0.53
KeD	10.2	25	0.67	-0.01	5.74	0.32
PeD	11.7	29	0.70	0.00	6.64	0.41
KeU	17.9	24	0.60	-0.15	4.82	0.14
KiD	17.9	23	0.66	-0.03	5.57	0.15

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609

Table 4

Assignment tests of each individual for six populations (up) and three genetic clusters (bottom) using GeneClass2. Values represent the percentage of individuals from the sampled population (row) to the assigned population (column). Bold indicates the percentage of self-assignment.

Sampled	Assigned	Cluster1		Cluster2		Cluster3	
		KiU	PeU	KiD	PeD	KeD	KeU
Cluster1	KiU	31.3	21.9	15.6	25.0	6.3	0.0
	PeU	20.0	33.3	0	40.0	6.7	0.0
	KiD	17.4	21.7	13.0	39.1	8.7	0.0
Cluster2	PeD	13.8	20.7	10.4	51.7	3.5	0.0
	KeD	16.0	24.0	8.0	32.0	20.0	0.0
Cluster3	KeU	12.5	50.0	20.8	12.5	4.2	0.0
Average		18.5	28.6	11.3	33.4	8.2	0.0

Sampled	Assigned	Cluster1		Cluster2		Cluster3	
Cluster1		61.9		38.1		0.0	
Cluster2		48.1		52.0		1.1	
Cluster3		47.8		52.2		0.0	
Average		52.6		47.4		0.0	

Figure Captions

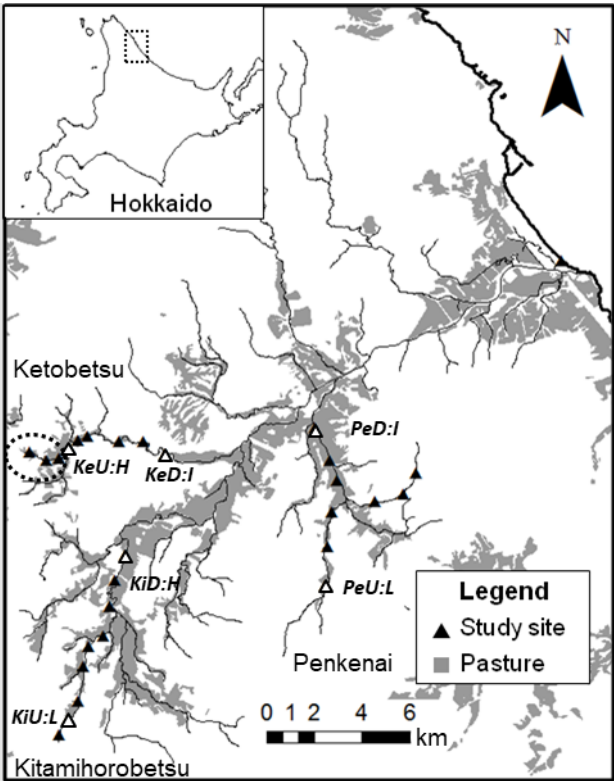
Fig. 1 Study sites for the examination of population dynamics (black and white triangles) and genetic analysis (white triangles). The six sites included in the genetic analysis were in the upstream and downstream regions of three streams (sites *KeU*, *KeD*, *KiU*, *KiD*, *PeU* and *PeD*). The letters (*L*, *I* and *H*) beside the site names indicate three levels of agricultural development: *L*: low % pasture (0-1 %), *I*: moderate (10-12 %) and *H*: high (approximately 18 %), which corresponds to population stability (see Methods). Sites enclosed by the dotted line in the upstream region of the Ketobetsu stream showed an absence of *S. marmorata* during all sampling occasions.

Fig. 2 Relationships between pasture cover within a catchment area and the abundance and resistance of the *S. marmorata* population. White circles indicate sites where genetic samples were collected (*KiU*, *KiD*, *PeU*, *PeD*, *KeU*, *KeD*). Solid lines are the lines predicted by the GLM. The resistance index is calculated by post-flood abundance/preflood abundance. (see Methods). Mar; March, Nov; November.

Fig. 3 Genetic clustering of six populations by UPGMA based on D_{sw} distance. Numbers indicate bootstrap support.

Fig. 4 Effective number of migrants (N_{em}) among genetic clusters. The thickness of grey arrows represents N_{em} .

Fig. 5 Effective number of migrants (N_{em}) between up- and downstream sites within each stream. The thickness of the grey arrows represents N_{em} .



635
636 Fig. 1

637

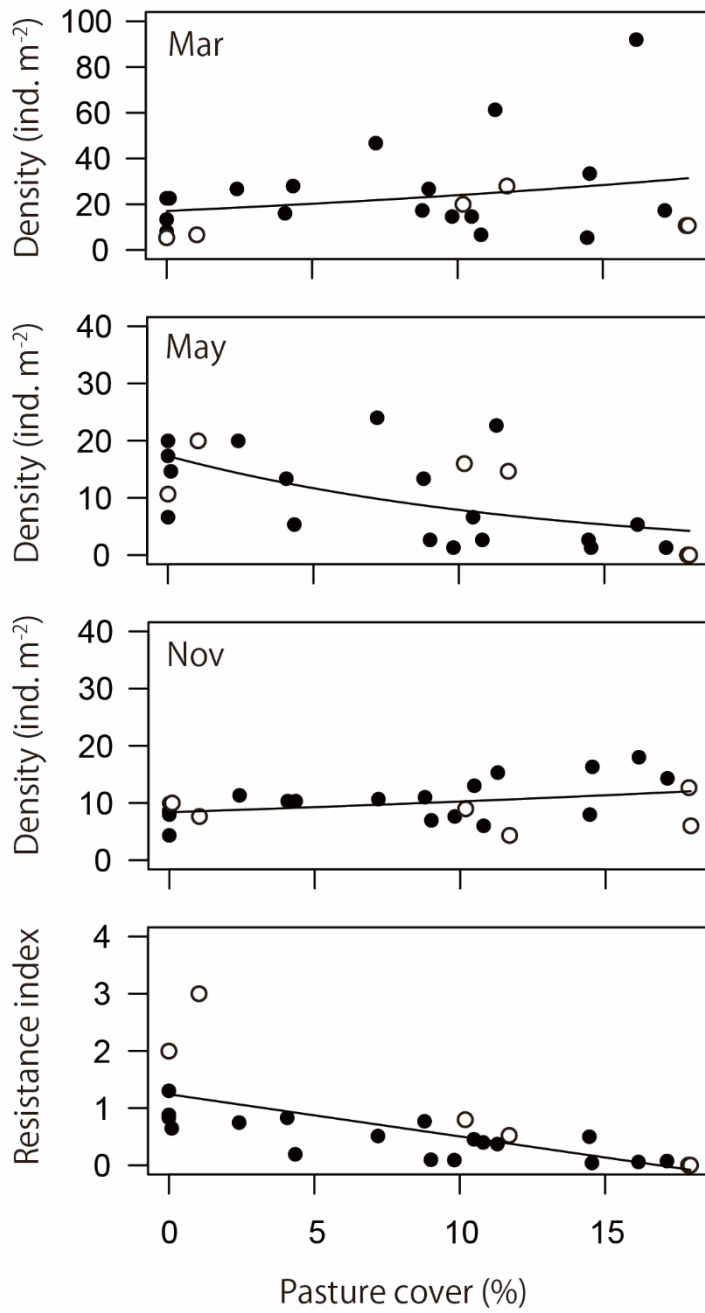


Fig. 2

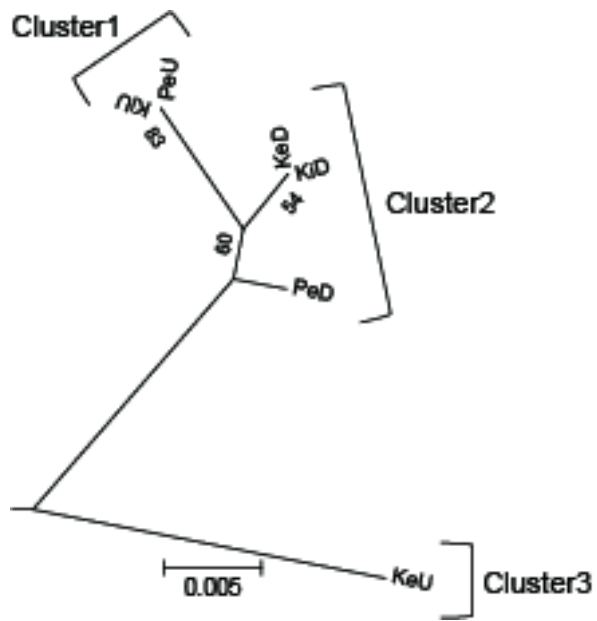


Fig. 3

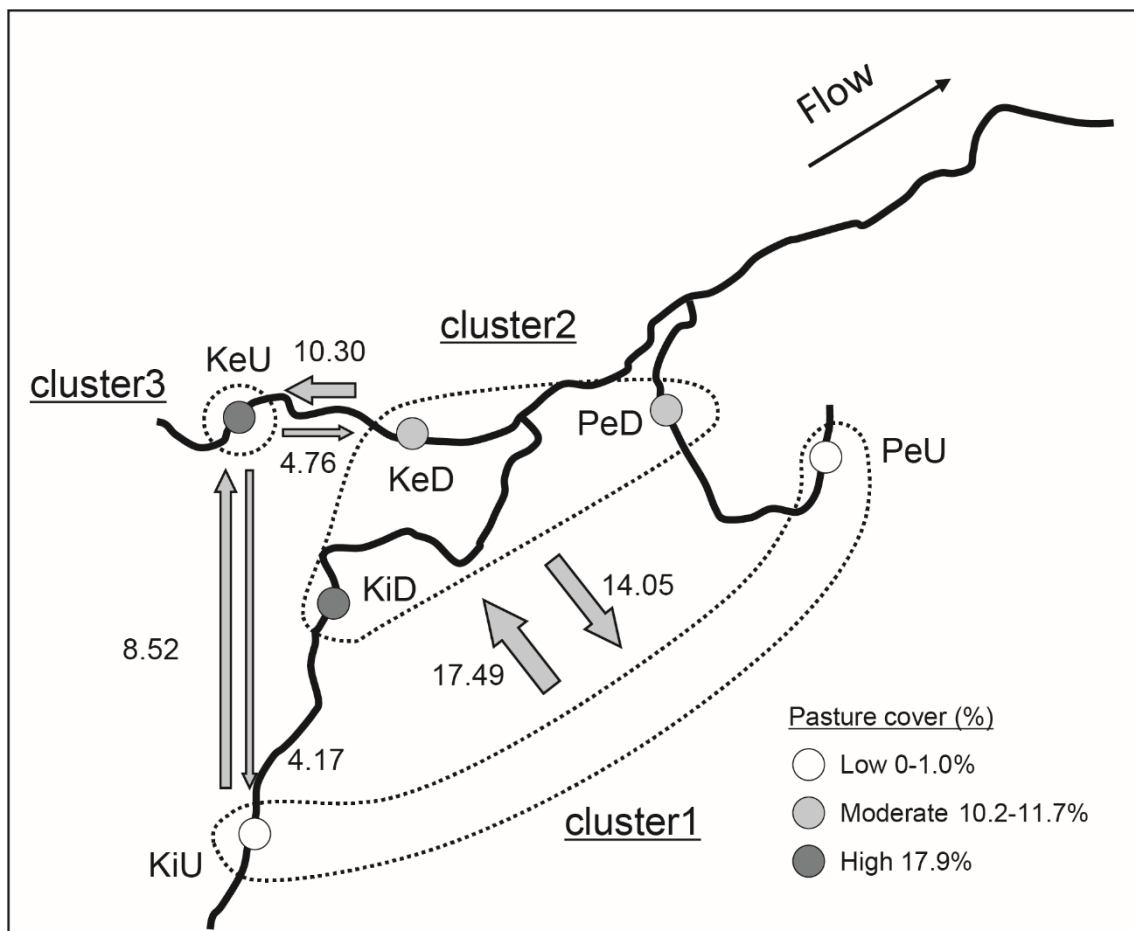
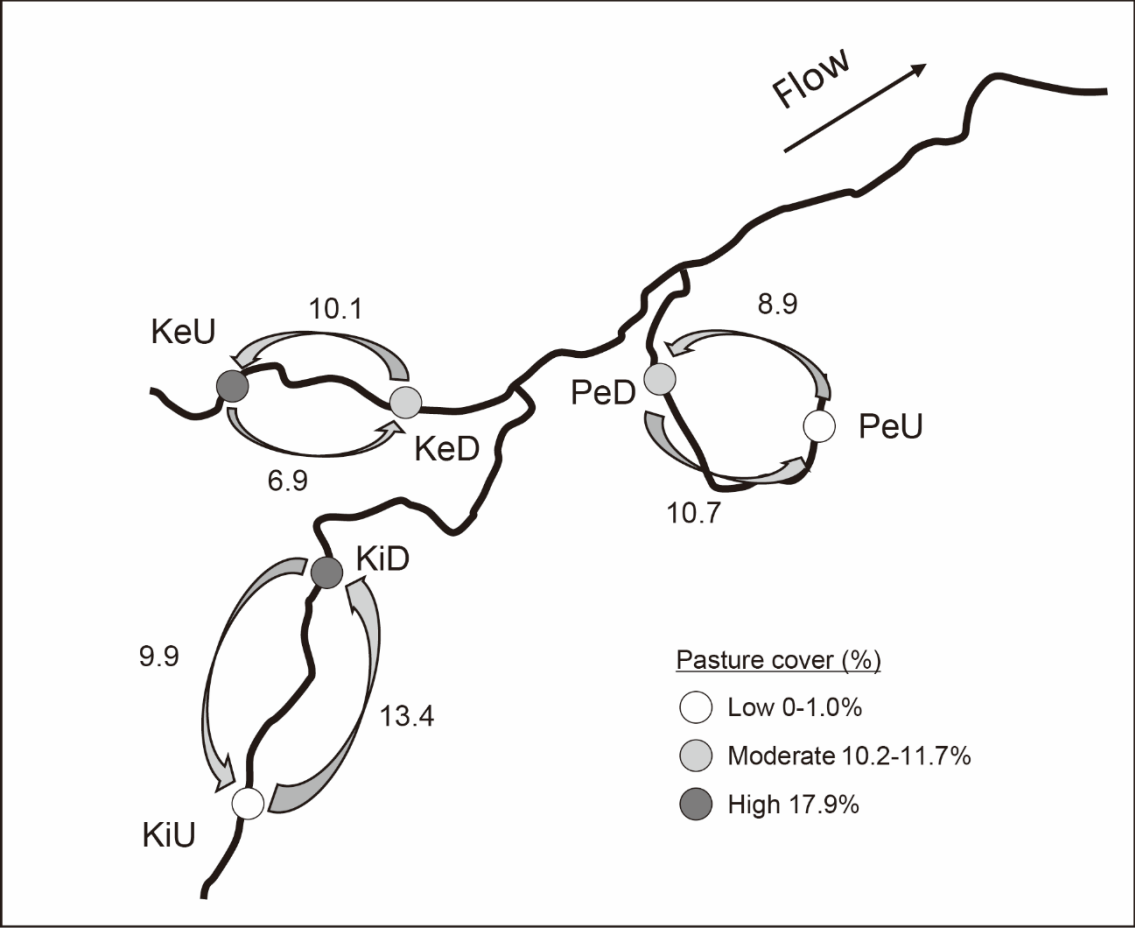


Fig. 4

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648 Fig. 5