



Title	Inferring future changes in gene flow under climate change in riverscapes : a pilot case study in fluvial sculpin
Author(s)	Nakajima, Souta; Suzuki, Hiroaki; Nakatsugawa, Makoto; Matsuo, Ayumi; Hirota, Shun K.; Suyama, Yoshihisa; Nakamura, Futoshi
Citation	Landscape Ecology(38), 1351-1362 https://doi.org/10.1007/s10980-023-01633-x
Issue Date	2023-03-15
Doc URL	http://hdl.handle.net/2115/91323
Rights	This version of the article has been accepted for publication, after peer review (when applicable) and is subject to Springer Nature 's AM terms of use, but is not the Version of Record and does not reflect post-acceptance improvements, or any corrections. The Version of Record is available online at: http://dx.doi.org/10.1007/s10980-023-01633-x
Type	article (author version)
File Information	CottusRG.pdf



[Instructions for use](#)

1 **Inferring future changes in gene flow under climate change in riverscapes: a pilot case**
2 **study in fluvial sculpin**

3

4 Souta Nakajima^{1,2,*}, Hiroaki Suzuki^{3,4}, Makoto Nakatsugawa³, Ayumi Matsuo⁵, Shun K. Hirota^{5,6},
5 Yoshihisa Suyama⁵, Futoshi Nakamura¹

6

7 ¹ Graduate School of Agriculture, Hokkaido University, Kita-ku N9W9, Sapporo, Hokkaido 060-8589,
8 Japan

9 ² Present address: Water Environment Research Group, Public Works Research Institute, Minamihara
10 1-6, Tsukuba, Ibaraki 305-8516, Japan

11 ³ Graduate School of Engineering, Muroran Institute of Technology, Mizumoto-cho 27-1, Muroran,
12 Hokkaido 050-8585, Japan

13 ⁴ Research Institute of Energy, Environment and Geology, Hokkaido Research Organization, Kita-ku
14 N19W12, Sapporo, Hokkaido 060-0819, Japan

15 ⁵ Graduate School of Agricultural Science, Tohoku University, Yomogida 232-3, Naruko-onsen,
16 Osaki, Miyagi 989-6711, Japan

17 ⁶ Present address: Botanical Gardens, Osaka Metropolitan University, Kisaichi 2000, Katano, Osaka
18 576-0004, Japan

19

20 * Corresponding author

21 Souta Nakajima: n.souta891@gmail.com

22 Watershed Restoration Team, Water Environment Research Group, Public Works Research Institute,
23 Minamihara 1-6, Tsukuba, Ibaraki 305-8516, Japan

24 Phone: +81-29-879-6775, Fax: +81-29-869-5082

25

26 ORCID

27 Souta Nakajima: <https://orcid.org/0000-0003-3701-5428>

28 Shun K. Hirota: <https://orcid.org/0000-0002-6104-1119>

29 Yoshihisa Suyama: <https://orcid.org/0000-0002-3136-5489>

30 Futoshi Nakamura: <https://orcid.org/0000-0003-4351-2578>

31

32 **Acknowledgments**

33 We thank Nobuo Ishiyama for his cooperation in validating the hydrological model. This study is

34 partly supported by the research fund for the Ishikari and Tokachi Rivers provided by the Ministry of

35 Land, Infrastructure, Transport and Tourism of Japan.

36

37 **Abstract**

38 **Context:** Global climate change poses a significant threat to the habitat connectivity of cold-water-
39 adapted organisms, leading to species extinctions. If gene flow can be modeled by landscape variables,
40 changes in connectivity among populations could be predicted. However, in dendritic and
41 heterogeneous stream ecosystems, few studies have estimated the changes in gene flow from genetic
42 data, in part due to the difficulty in applying landscape genetics methods and accessing water
43 temperature information.

44 **Objectives:** Inferring the determinants and future changes of the gene flow in the cold-water adapted
45 fluvial sculpin *Cottus nozawae* using a recently developed model-based riverscape genetics technique
46 and a hydrological model for estimating water temperature.

47 **Methods:** The strength of gene flow on each stream section was modeled by watershed-wide
48 riverscape variables and genome-wide SNP data for *C. nozawae* in the upper reaches of the Sorachi
49 River, Hokkaido, Japan. Future changes in gene flow were inferred by this model and hydrologically
50 estimated water temperatures under the high greenhouse gas concentration scenario (IPCC RCP8.5).

51 **Results:** Stream order, water temperature, slope, and distance were selected as riverscape variables
52 affecting the strength of gene flow in each stream section. In particular, the trend of greater gene flow
53 in sections with higher stream order and lower temperature fluctuations or summer water temperatures
54 was pronounced. The map from the model showed that gene flow is overall prevented in small
55 tributaries in the southern area, where spring-fed environments are less prevalent. Estimating future
56 changes, gene flow was predicted to decrease dramatically at the end of the 21st century.

57 **Conclusions:** Our results demonstrated that the connectivity of cold-water sculpin populations is
58 expected to decline dramatically in a changing climate. Riverscape genetic modeling is useful for
59 gaining information on population connectivity that does not fully coincide with habitat suitability.

60

61 **Keywords**

62 model-based riverscape genetics; cold-water fish; *Cottus*; water temperature; global warming

63

64 **Introduction**

65 Global climate change modifies water temperatures and flow regimes, the two key habitat factors
66 affecting freshwater species, posing a critical threat to stream ecosystems (Barbarossa et al. 2021). The
67 spatial distribution of species' suitable habitats shifts with environmental changes, and population
68 fragmentation due to impassable environments may eventually result in local and/or species
69 extinctions (Woodward et al. 2010). Numerous studies have predicted changes in species distributions
70 and suitable habitats of stream organisms (Elith and Leathwick 2009; Comte et al. 2012; Ishiyama et
71 al. 2023; Rahel et al. 1996), but how will the actual population connectivity and migration potential
72 change?

73 Gene flow represents the functional connectivity among wild populations and is critical in
74 species viability (Kottler et al. 2021; Manel and Holderegger 2013). The strength of gene flow is
75 usually discussed individually from the observed genetic structure, but if gene flow could be modeled
76 by landscape variables, the gained knowledge regarding gene flow could be generalized and used to
77 predict its future changes (McRae and Beier 2007). The relationships between gene flow and
78 landscape variables have been investigated in the field of landscape genetics (Balkenhol et al. 2015).
79 However, most analytical techniques developed in landscape genetics exert only poor power in linear
80 and dendritic stream ecosystems (Davis et al. 2018; Chafin et al. 2021), making it difficult to predict
81 future changes in gene flow in riverscapes. Even in streams, regression models can be created by
82 contrasting a genetic distance matrix against pairwise differences in local conditions (Grummer et al.
83 2019), but this approach fails to account for the network architecture and for the attributes in all the
84 spaces that individuals must pass through when traveling between sampling sites (Davis et al. 2018;
85 White et al. 2020; Escalante et al. 2020). Another versatile approach to investigating the effects of
86 landscape elements on gene flow is defining "landscape resistance" surfaces and assessing the
87 relationship between genetic distance and cumulative resistance between populations (isolation by
88 resistance; IBR (McRae 2006)). Although this idea has been applied to studies on stream ecosystems
89 in several cases (e.g., Inoue and Berg 2017; Oliveira et al. 2019; Landguth et al. 2016; Escalante et al.
90 2018), the landscape resistance must be parametrized *a priori* through expert opinion or other
91 empirical methods (e.g., using the inverse of species distribution model estimates) (Spear et al. 2015;

92 Zeller et al. 2012). To understand the gene flow itself, its determinants should be identified directly
93 from genetic data (Sartor et al. 2022; Wasserman et al. 2010). Fortunately, alternative methods for
94 modeling gene flow from genetic data within a spatially explicit graph-theoretic framework have been
95 developed rapidly in recent years (White et al. 2020; Chafin et al. 2021). Although not yet practically
96 applied to predictions under environmental changes, we thought that these “riverscape genetics”-
97 dedicated methods are the key to determining landscape resistance and modeling current and future
98 gene flow.

99 Another theme that makes riverscape genetics challenging is the data availability of key
100 environmental elements such as water temperatures. For terrestrial organisms, globally available
101 climate data such as WorldClim (Hijmans et al. 2005) are commonly used to estimate the effects of
102 climate change. However, data on current and future water temperatures that are critical for stream
103 organisms are difficult to obtain as are data on flow rate. Although some studies have used air
104 temperature data as a surrogate of water temperatures (Almodóvar et al. 2012), water temperatures do
105 not actually coincide with air temperatures. In particular, local spatial heterogeneity in water
106 temperatures caused by groundwater discharge and other factors is truly a source of ecosystem
107 diversity and resilience to climate change that cannot be ignored (Koizumi and Maekawa 2004;
108 Nakajima et al. 2021; Ishiyama et al. 2023; Nakamura 2022). Therefore, it is critical in riverscapes to
109 utilize water temperature information considering the spatial heterogeneity generated by
110 hydrogeological factors.

111 *Cottus nozawae* is a cold-water-adapted sculpin inhabiting northern Japan. Since the
112 distribution and ecology of this species are highly influenced by summer water temperatures (Yagami
113 and Goto 2000), available habitats are expected to decrease significantly under climate change (Suzuki
114 et al. 2021). At a local scale, streams with low summer water temperatures characterized by spring-fed
115 environments have been shown to display high population densities and to be the source of individuals
116 in a watershed (Suzuki et al. 2021; Nakajima et al. 2021). Under ongoing climate change, the
117 migration of this species is expected to be frequently blocked by unsuitable habitats, resulting in
118 population fragmentation and shrinkage. To sustain the species into the future, it is critical to
119 accurately predict the relationship between population connectivity and climate-related variables. Such

120 predictions will contribute to the advancement of climate change adaptation measures for this species,
121 such as by identifying sections where stream continuity should be ensured.

122 Considering the challenges of data availability and analysis in riverscape genetics, we thought
123 that the recently developed model-based riverscape genetics approaches and physics-based
124 hydrological model to estimate water temperatures would enable the modeling and future prediction of
125 gene flow in cold-water fish. The aims of this study are (i) to identify the factors determining the gene
126 flow of *C. nozawae* in the stream network, (ii) to model the strength of gene flow using riverscape
127 variables and predict its future changes, and (iii) to discuss the applicability of riverscape genetic
128 modeling in conservation ecology.

129

130 **Material and Methods**

131 *Study sites and sampling*

132 In 2019, small pieces of fin tissue were sampled from 376 individuals of *C. nozawae* caught by
133 electrofishing (model 12-B Backpack Electrofisher; Smith-Root Inc.) at 13 sites located in the
134 upstream section of the Sorachi River, Hokkaido, Japan (Fig. 1; Table S1). Because no river-crossing
135 structures that would obviously prevent fish migration are present between sampling sites, this area is
136 considered suitable for evaluating the effects of riverscape variables. Regarding the environmental
137 conditions, the tributaries in the northern volcanic watersheds have spring-fed environments with
138 stable water temperatures and flow regimes (García Molinos et al. 2022; Ishiyama et al. 2023). For
139 riverscape genetic modeling, the stream network among sampling sites was viewed as a graph
140 consisting of 24 “nodes” and 23 “edges” (Fig. 2a). We defined “nodes” as the sampling sites and
141 major tributary confluences between them, and analysis was conducted with “edges”, the stream
142 segments between adjacent nodes, as units.

143

144 *Genetic data*

145 Genomic DNA was extracted using the QIAGEN DNeasy Blood and Tissue Kit (QIAGEN
146 Inc.). In this study, we used the multiplexed ISSR genotyping by sequencing (MIG-seq) method
147 (Suyama and Matsuki 2015; Suyama et al. 2022), a technique in which loci between two microsatellite

148 regions are amplified and neutral genome-wide single nucleotide polymorphisms (SNPs) are detected.
149 A MIG-seq library preparation and read quality filtering were performed according to the protocol
150 described in Suyama et al. (2022), with the modification that two runs were conducted and the
151 obtained data were combined after quality filtering. In addition, quality filtering was performed on 71
152 bases with six 5'-end bases and three 3'-end bases removed. After quality filtering, SNP selection was
153 performed using STACKS 2.41 (Catchen et al. 2013). First, the reads were grouped to each locus
154 using the *ustacks*, *cstacks*, *sstacks*, *tsv2bam*, and *gstacks* commands with the following parameters
155 recommended by Paris et al. (2017): minimum depth option creating a stack (m) = 3, maximum
156 distance between stacks (M) = 2, maximum mismatches between loci when building the catalog
157 (n) = 2, and number of mismatches allowed to align secondary reads (N) = 4. From the derived dataset
158 of assembled loci, SNPs were detected using the *populations* commands under the following criteria:
159 only loci present at a rate of more than 80% of individuals within all populations were extracted (-p 13
160 -r 0.8); the minimum minor allele frequency was 5% (--min-maf 0.05); sites showing excess
161 heterozygosity were removed (--max-obs-het 0.6); and the output was limited to one SNP per locus (--
162 write-single-snp). After filtering, 212 SNPs were obtained.

163 For populations in each sampling site, the expected heterozygosity (H_E) and fixation index
164 (F_{IS}) were calculated using the *populations* command in STACKS. Significant deviations from Hardy–
165 Weinberg equilibrium, as indicated by F_{IS} deviating from zero, were tested by 1000 randomizations
166 using FSTAT 2.9.4 (Goudet 1995). Genetic differentiation among populations was assessed by G_{ST}
167 (Nei 1973) and D_{PS} (Bowcock et al. 1994). D_{PS} is the genetic distance based on the dissimilarities of
168 population allele pools and reflects gene flow over a shorter timescale (approximately 10 generations;
169 Landguth et al. 2010; Leroy et al. 2018), whereas G_{ST} is assumed to reflect long-term gene flow
170 (Holsinger and Weir 2009). G_{ST} was calculated using GenAlEx 6.51 (Peakall and Smouse 2012), and
171 D_{PS} was calculated using the package graph4lg (Savary et al. 2021) in R 3.6.0 (R Core Team 2019).
172 To understand the general patterns of population structure, STRUCTURE 2.3.4 (Pritchard et al. 2000)
173 was performed in the setting of the admixture and allele frequency correlated model with previous
174 sampling location information (LOCPRIOR; Hubisz et al. 2009). The algorithm was run 10 times for
175 each K from 1 to 10 with a burn-in of 20,000 followed by 30,000 MCMC replicates. The program

176 CLUMPAK (Kopelman et al. 2015) was then used to summarize the results for each K. STRUCTURE
177 HARVESTER (Earl and vonHoldt 2012) was employed to calculate the probability of the data for
178 each K (LnP(D); Pritchard et al. 2000), the corresponding standard deviation, and the ΔK (Evanno et
179 al. 2005).

180

181 *Riverscape data*

182 Riverscape variables were collected as a unit of edges. Edge length, slope, stream orders, and
183 catchment area were calculated in ArcGIS 10.7.1 (ESRI Inc.) using National Land Numerical
184 Information (nlftp.mlit.go.jp) from the Ministry of Land, Infrastructure, Transport and Tourism
185 (MLIT) of Japan. Flow rate and water temperature were estimated by a hydrological model based on
186 Suzuki et al. (2022), which considers differences in groundwater discharge depending on catchment
187 geology (see Appendix 1 for details). Briefly, the daily flow rate on the stream in each 1 km mesh was
188 reproduced by four-layered tank models (Sugawara 1979), and the flow and heat flux were tracked
189 along the streamflow. Importantly, different tank parameters were given for the volcanic areas and
190 other areas, based on validation using measured water temperature data from field surveys at multiple
191 sites in the study area. Flow rate and water temperature from September 2018 to August 2019 were
192 reproduced and used to calculate the riverscape variables. In future predictions, 1 km-downscaled data
193 on meteorological elements (Ueda et al. 2020), calculated under the climate data projected in the
194 representative concentration pathway scenario 8.5 (RCP8.5) in the IPCC 5th Assessment (IPCC 2014),
195 was used to derive the input water amount to the tank model. We used the mean of the predicted
196 variables for the years 2081 to 2100 (all from September to next August) as future riverscape
197 variables.

198

199 *Gene flow analysis*

200 We probabilistically modeled the relative migration rate (edge passability) of each edge as a function
201 of riverscape variables using the “BGR model” (White et al. 2020). This is a novel method that can
202 model bidirectional gene flow in stream networks using genetic distance matrices as input data and
203 riverscape variables as explanatory variables, rigorously accounting for the spatial autocorrelation

204 structure of stream networks using a graph-theoretical framework and a spatial autoregressive model.
205 Specifically, the nearly homogeneous stream segments (delimited by nodes that are sampling sites or
206 major tributary confluences) were defined as edges, and the relative migration rate (edge passability;
207 w_{ij}) of each edge linking nodes i and j was estimated as a function of k riverscape variables ($x_{ij1}, x_{ij2},$
208 \dots, x_{ijk}) and the corresponding parameters ($\beta_1, \beta_2, \dots, \beta_k$) as:

$$209 \quad w_{ij} = \exp(\beta_0 + \sum_k \beta_k x_{ijk})$$

210 where β_0 is the intercept term. Here, all riverscape variables were normalized from 0 to 1. The
211 posterior distribution of parameters $\beta_0, \beta_1, \dots, \beta_k$ was estimated by a Markov Chain Monte Carlo
212 (MCMC) sampler, to fit the input genetic data. The mathematics linking w_{ij} to genetic distance are
213 described in Peterson et al. (2019).

214 The BGR model was run in R. We used G_{ST} and D_{PS} as genetic distances and 10 possible
215 riverscape variables (Table 1; Fig. S1) as covariates x_{ijk} . All variables except direction are symmetric.
216 For each summary statistic, forward selections were conducted based on the deviance information
217 criterion (DIC). Variables were added until the DIC no longer decreased by 7 or more (Cain and
218 Zhang 2019). At each step of the forward selection, the variables that were highly correlated
219 (Pearson's $r > 0.7$) with other variables already included in the model were not added to the model.
220 Models with fewer than four variables were run for 50,000 MCMC iterations and parameters were
221 estimated after 25,000 burn-in. Models with four or more variables were run for 100,000 iterations
222 including 50,000 burn-in. After the final model was identified, we conducted a long run with 500,000
223 iterations including 200,000 burn-in, to accurately estimate the β values and 95% credible intervals.
224 Landscape resistance, calculated as the inverse of w_{ij} of each edge, was estimated and mapped from
225 the selected models. To evaluate the estimates, the correlations between genetic distances and
226 estimated landscape resistance (sum of edges between populations) were calculated by Mantel tests
227 with 9999 permutations, and compared to the correlations between genetic distances and waterway
228 geographical distance. The Mantel tests were conducted using the package VEGAN 2.5.6 (Oksanen et
229 al. 2019) in R. Future landscape resistance was inferred by substituting the future water temperature
230 variable into the final BGR model. At this stage, we used the model derived from D_{PS} because G_{ST}

231 displays long-term patterns and D_{PS} is more likely to reflect current changes in gene flow.

232

233 **Results**

234 The level of H_E was similar across the watershed (ranged from 0.241–0.272), and F_{IS} ranged from -
235 0.012–0.023 with no populations deviating significantly from zero (Table S1). The average G_{ST} was
236 0.029 (ranged from 0.000–0.047; Table S2) and D_{PS} was 0.087 (ranged from 0.050–0.135). In the
237 STRUCTURE, while $\ln P(D)$ for each K increased progressively, ΔK was highest at $K = 2$, and locally
238 maximum at $K = 6$ (Fig. S2). Populations in the southern area were grouped into distinct clusters from
239 low K , and as K increased, populations in other tributaries were also mixed with geographically
240 uneven clusters. The strength of population structure differed geographically (Fig. 2a), but the factors
241 determining this difference are not known by the STRUCTURE. From the forward selection of the
242 model explaining the strength of gene flow, Shreve's stream order, water temperature fluctuation,
243 slope, and edge length were selected for G_{ST} , and Strahler's stream order and summer water
244 temperature were selected for D_{PS} , in this order (Tables 2 and S3). In both cases, the first and second
245 variables added to the model were the stream order and water temperature, respectively. While
246 different types of variables were selected for G_{ST} and D_{PS} (Shreve's or Strahler's; summer water
247 temperature or water temperature fluctuation), these results show the importance of the stream order
248 and water temperature on the strength of gene flow. The stream orders had a positive effect on gene
249 flow, while the water temperature fluctuation or summer water temperature had a negative effect. The
250 effect (β) of the water temperature on gene flow was higher in D_{PS} than in G_{ST} . In G_{ST} , the slope and
251 edge length were also selected and had negative effects, indicating their relevance to long-term gene
252 flow. Geographically, the southern upstream area had generally higher landscape resistance (lower
253 gene flow) than the main stream, while in the northern volcanic area, landscape resistance was not so
254 high even upstream (Fig. 2). The Mantel tests between the genetic distances and estimated landscape
255 resistance suggested significant relationships ($r = 0.46$, $p < 0.05$ for G_{ST} ; $r = 0.60$, $p < 0.01$ for D_{PS}),
256 and the correlations were much higher than those between the genetic and geographic distances (Fig.
257 3). The future prediction indicated that the landscape resistance would increase overall from the
258 current levels. Some sections in the main stream and in the upper reaches in the volcanic area were

259 estimated to exhibit as high landscape resistance levels as the present southern upstream area. The
260 southern upstream area was projected to display very high resistance.

261

262 **Discussion**

263 In this study, we succeeded in modeling and future predicting of gene flow of *C. nozawae* in the
264 stream network. Although there are still challenges in the modeling technique (e.g., simplicity of
265 model assumptions, difficulty of model evaluation, etc.), the modeled landscape resistance explained
266 the genetic distances well (Fig. 3); the strength of gene flow could be largely explained by riverscape
267 variables.

268 It was a somewhat unexpected result that the stream order was identified as the variable with
269 the strongest effect on gene flow. Previous studies of cold-water fish have reported both higher and
270 lower gene flow in streams with higher stream orders (Aunins et al. 2015; Escalante et al. 2018; White
271 et al. 2020). Within the arbitrary study areas, main streams tend to have higher water temperatures and
272 are often unsuitable environments for cold-water fish. On the other hand, in dendritic stream
273 structures, confluences are often known to be stable gene accumulation and source points for stream
274 organisms (Grant et al. 2007; Paz-Vinas and Blanchet 2015), and the downstream passage of those
275 organisms may result in higher gene flow in higher-order streams. In addition, as the main stream
276 tends to be more severely affected by flooding (Han et al. 2007; Koizumi et al. 2013), individuals,
277 especially those of low-mobility species, may have a greater chance of being flushed. There may be
278 differences regarding which processes are predominant depending on the studied species or areas.
279 Summer water temperature (or water temperature fluctuation in G_{ST}) negatively affected gene flow.
280 This is probably because streams with high summer water temperatures and large fluctuations are not
281 suitable environments for *C. nozawae* (Suzuki et al. 2021), making successful dispersal difficult.
282 While it is not uncommon for studies of cold-water fishes to implicate an association between gene
283 flow and water temperature-related variables (Kanno et al. 2011; Escalante et al. 2018; Hand et al.
284 2016), the present study was able to represent this pattern using more realistic water temperature
285 information. The model from G_{ST} also included the slope and edge length, but the model from D_{PS} did
286 not. We found that topography and distance affected the formation of the long-term population

287 structure as in many other systems (Kanno et al. 2011; Caldera and Bolnick 2008), but that most of the
288 current gene flow can be explained by the stream order and water temperature. The upstream-
289 downstream direction did not affect gene flow, probably because environmental conditions influence
290 the direction of gene flow (Nakajima et al. 2021).

291 Maps displaying modeled landscape resistance from G_{ST} and D_{PS} were visually similar (Fig.
292 2), indicating that the pattern has probably been maintained for a long time. Overall, gene flow is
293 prevented in small tributaries in the southern area. This area displays higher water temperature
294 fluctuations than the northern volcanic area where spring-fed environments are more prevalent
295 (Ishiyama et al. 2023); gene flow in the southern area is probably suppressed by the effects of water
296 temperature. When comparing this geographical pattern with the STRUCTURE barplots, the upper
297 reaches in the non-volcanic area where gene flow is prevented roughly corresponded to the areas
298 where a strong population structure was observed. While the reason for the heterogeneity in the
299 strength of population structure could not be known by the STRUCTURE, a possible explanation was
300 explicitly presented in the gene flow analysis.

301 Under the RCP8.5 scenario, reduced gene flow and increased landscape resistance across the
302 watershed were predicted (Fig. 2d). Since the studied species exhibited a clear genetic structure only
303 in the southern area, the prediction that the northern area will have the same level of gene flow as the
304 present southern area indicates that each tributary within the watershed may experience genetic
305 fragmentation in the future. Nevertheless, gene flow in the northern area was expected to be
306 maintained spatially continuously to some extent, indicating that streams with volcanic watersheds are
307 important for ensuring population connectivity under climate change. A previous study suggested that
308 streams with low summer temperatures behave as source habitats in the watershed (Nakajima et al.
309 2021). Our study showed that these streams may serve not only as source habitats but also as
310 migration pathways in the watershed. As a scenario analysis, Inoue and Berg (2017) considered
311 landscape resistance to be the inverse of the species distribution model (SDM) estimates and predicted
312 that an increased landscape resistance would reduce the gene flow of freshwater bivalves in the future.
313 This is a valuable study that attempts to predict future changes in gene flow; however, it is known that
314 the habitat suitability maps created by SDMs provide poor estimates of genetic resistance, because of

315 the conceptual differences between habitat selection and entire gene flow (Wasserman et al. 2010,
316 2012; Sator et al. 2022; Mateo-Sánchez 2015). Actually, in *C. nozawae*, the SDM created in Suzuki et
317 al. (2021) indicated that the catchment area, analogous to the stream order, had a negative effect on the
318 occurrence of this species, in contrast to the gene flow characteristics estimated in our study.
319 Therefore, genetic population connectivity should be considered separately from habitat suitability.

320 The present study is novel in that gene flow was modeled using riverscape variables identified
321 from genetic data and including water temperature. Our results showed that gene flow in the cold-
322 water sculpin is expected to decrease dramatically in response to a changing climate. Therefore, under
323 ongoing climate change, it is important to maintain habitat continuity within the distribution ranges. In
324 particular, it is necessary to consider that the risk is high in sections where water temperature
325 fluctuations are large (such as non-volcanic watersheds). Additionally, while main streams may be less
326 suitable as habitats, they are important as migration corridors. No structures such as weirs should be
327 installed so that drifted individuals can quickly enter suitable habitats.

328 To obtain more robust results, it would be desirable to increase the number of sampling
329 populations. This study has the potential for further development. For example, demography
330 simulations using inferred landscape resistance (Landguth et al. 2010, 2016) could reveal population
331 viability. Also, combined with habitat quality analyses such as SDMs, population connectivity could
332 be quantified for more detailed predictions from the viewpoint of habitat availability (Saura and
333 Pascual-Hortal 2007). We hope that riverscape genetic modeling will be applied to predict the
334 consequences of environmental changes on a variety of freshwater organisms.

335

336 **References**

- 337 Almodóvar A, Nicola GG, Ayllón D, Elvira B (2012) Global warming threatens the persistence of
338 Mediterranean brown trout. *Glob Chang Biol* 18:1549–1560. [https://doi.org/10.1111/j.1365-
339 2486.2011.02608.x](https://doi.org/10.1111/j.1365-2486.2011.02608.x)
- 340 Aunins AW, Petty JT, King TL et al (2015) River mainstem thermal regimes influence population
341 structuring within an appalachian brook trout population. *Conserv Genet* 16:15–29.
342 <https://doi.org/10.1007/s10592-014-0636-6>

343 Balkenhol N, Cushman SA, Storfer A, Waits LP (2015) Introduction to landscape genetics - concepts,
344 methods, applications. In: Balkenhol N, Cushman SA, Storfer A, Waits LP (ed) Landscape
345 Genetics. Wiley, New York, pp 1–8

346 Barbarossa V, Bosmans J, Wanders N, et al (2021) Threats of global warming to the world’s
347 freshwater fishes. Nat Commun 12:1701. <https://doi.org/10.1038/s41467-021-21655-w>

348 Bowcock AM, Ruiz-Linares A, Tomfohrde J, et al (1994) High resolution of human evolutionary trees
349 with polymorphic microsatellites. Nature 368:455–457. <https://doi.org/10.1038/368455a0>

350 Cain MK, Zhang Z (2019) Fit for a Bayesian: An evaluation of PPP and DIC for structural equation
351 modeling. Struct Equ Model 26:39–50. <https://doi.org/10.1080/10705511.2018.1490648>

352 Caldera EJ, Bolnick DI (2008) Effects of colonization history and landscape structure on genetic
353 variation within and among threespine stickleback (*Gasterosteus aculeatus*) populations in a
354 single watershed. Evol Ecol Res 10:575–598

355 Catchen J, Hohenlohe PA, Bassham S, et al (2013) Stacks: An analysis tool set for population
356 genomics. Mol Ecol 22:3124–3140. <https://doi.org/10.1111/mec.12354>

357 Chafin TK, Mussmann SM, Douglas MR, Douglas ME (2021) Quantifying isolation-by-resistance and
358 connectivity in dendritic ecological networks. bioRxiv.
359 <https://doi.org/10.1101/2021.03.25.437078>

360 Comte L, Buisson L, Daufresne M, Grenouillet G (2012) Climate-induced changes in the distribution
361 of freshwater fish: observed and predicted trends. Freshw Biol 58:625–639.
362 <https://doi.org/10.1111/fwb.12081>

363 Davis CD, Epps CW, Flitcroft RL, Banks MA (2018) Refining and defining riverscape genetics: How
364 rivers influence population genetic structure. WIREs Water 5:e1269.
365 <https://doi.org/10.1002/wat2.1269>

366 Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: A website and program for visualizing
367 STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361.
368 <https://doi.org/10.1007/s12686-011-9548-7>

369 Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction
370 across space and time. Annu Rev Ecol Evol Syst 40:677–697.

371 <https://doi.org/10.1146/annurev.ecolsys.110308.120159>

372 Escalante MA, García-De León FJ, Ruiz-Luna A et al (2018) The interplay of riverscape features and
373 exotic introgression on the genetic structure of the Mexican golden trout (*Oncorhynchus*
374 *chrysogaster*), a simulation approach. *J Biogeogr* 45:1500–1514.
375 <https://doi.org/10.1111/jbi.13246>

376 Escalante MA, Perrier C, García-De León FJ et al (2020) Genotyping-by-sequencing reveals the
377 effects of riverscape, climate and interspecific introgression on the genetic diversity and local
378 adaptation of the endangered Mexican golden trout (*Oncorhynchus chrysogaster*). *Conserv*
379 *Genet* 21:907–926. <https://doi.org/10.1007/s10592-020-01297-z>

380 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the
381 software STRUCTURE: A simulation study. *Mol Ecol* 14:2611–2620.
382 <https://doi.org/10.1111/j.1365-294X.2005.02553.x>

383 García Molinos J, Ishiyama N, Sueyoshi M, Nakamura F (2022) Timescale mediates the effects of
384 environmental controls on water temperature in mid- to low-order streams. *Sci Rep* 12:12248.
385 <https://doi.org/10.1038/s41598-022-16318-9>

386 Goudet J (1995) FSTAT (Version 1.2): a computer program to calculate F-statistics. *J Hered* 86:485–
387 486. <https://doi.org/10.1093%2Foxfordjournals.jhered.a111627>

388 Grant EHC, Lowe WH, Fagan WF (2007) Living in the branches: population dynamics and ecological
389 processes in dendritic networks. *Ecol Lett* 10:165–175. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2006.01007.x)
390 [0248.2006.01007.x](https://doi.org/10.1111/j.1461-0248.2006.01007.x)

391 Grummer JA, Beheregaray LB, Bernatchez L (2019) Aquatic landscape genomics and environmental
392 effects on genetic variation. *Trends Ecol Evol* 34:641–654.
393 <https://doi.org/10.1016/j.tree.2019.02.013>

394 Han CC, Tew KS, Fang LS (2007) Spatial and temporal variations of two cyprinids in a subtropical
395 mountain reserve – a result of habitat disturbance. *Ecol Freshw Fish* 16:395–403.
396 <https://doi.org/10.1111/j.1600-0633.2007.00227.x>

397 Hand BK, Muhlfeld CC, Wade AA et al (2016) Climate variables explain neutral and adaptive
398 variation within salmonid metapopulations: the importance of replication in landscape genetics.

399 Mol Ecol 25:689–705. <https://doi.org/10.1111/mec.13517>

400 Hijmans RJ, Cameron SE, Parra JL, et al (2005) Very high resolution interpolated climate surfaces for
401 global land areas. *Int J Climatol* 25:1965–1978. <https://doi.org/10.1002/joc.1276>

402 Holsinger KE, Weir BS (2009) Genetics in geographically structured populations: Defining,
403 estimating and interpreting F_{ST} . *Nat Rev Genet* 10:639–650. <https://doi.org/10.1038/nrg2611>

404 Hubisz MJ, Falush D, Stephens M, Pritchard JK (2009) Inferring weak population structure with the
405 assistance of sample group information. *Mol Ecol Resour* 9:1322–1332.
406 <https://doi.org/10.1111/j.1755-0998.2009.02591.x>

407 Inoue K, Berg DJ (2017) Predicting the effects of climate change on population connectivity and
408 genetic diversity of an imperiled freshwater mussel, *Cumberlandia monodonta* (Bivalvia:
409 Margaritiferidae), in riverine systems. *Glob Chang Biol* 23:94–107.
410 <https://doi.org/10.1111/gcb.13369>

411 IPCC (2014) Summary for policymakers. <https://www.ipcc.ch/report/ar5/wg2/>

412 Ishiyama N, Sueyoshi M, García Molinos J, et al (2023) Underlying geology and climate interactively
413 shape climate change refugia in mountain streams. *Ecol Monogr*.
414 <https://doi.org/10.1002/ecm.1566>

415 Kanno Y, Vokoun JC, Letcher BH (2011) Fine-scale population structure and riverscape genetics of
416 brook trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks.
417 *Mol Ecol* 20:3711–3729. <https://doi.org/10.1111/j.1365-294X.2011.05210.x>

418 Koizumi I, Kanazawa Y, Tanaka Y (2013) The fishermen were right: experimental evidence for
419 tributary refuge hypothesis during floods. *Zool Sci* 30:375–379.
420 <https://doi.org/10.2108/zsj.30.375>

421 Koizumi I, Maekawa K (2004) Metapopulation structure of stream-dwelling Dolly Varden charr
422 inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshw Biol*
423 49:973–981. <https://doi.org/10.1111/j.1365-2427.2004.01240.x>

424 Kopelman NM, Mayzel J, Jakobsson M, et al (2015) Clumpak: A program for identifying clustering
425 modes and packaging population structure inferences across K. *Mol Ecol Resour* 15:1179–1191.
426 <https://doi.org/10.1111/1755-0998.12387>

427 Kottler EJ, Dickman EE, Sexton JP, et al (2021) Draining the swamping hypothesis: little evidence
428 that gene flow reduces fitness at range edges. *Trends Ecol Evol* 36:533–544.
429 <https://doi.org/10.1016/j.tree.2021.02.004>

430 Lamphere BA, Blum MJ (2012) Genetic estimates of population structure and dispersal in a benthic
431 stream fish. *Ecol Freshw Fish* 21:75–86. <https://doi.org/10.1111/j.1600-0633.2011.00525.x>

432 Landguth EL, Bearlin A, Day CC, Dunham J (2016) CDMetaPOP: an individual-based, eco-
433 evolutionary model for spatially explicit simulation of landscape demogenetics. *Methods Ecol*
434 *Evol* 8:4–11. <https://doi.org/10.1111/2041-210X.12608>

435 Landguth EL, Cushman SA, Schwartz MK, et al (2010) Quantifying the lag time to detect barriers in
436 landscape genetics. *Mol Ecol* 19:4179–4191. <https://doi.org/10.1111/j.1365-294X.2010.04808.x>

437 Leroy G, Carroll EL, Bruford MW et al (2018) Next-generation metrics for monitoring genetic erosion
438 within populations of conservation concern. *Evol Appl* 11:1066–1083.
439 <https://doi.org/10.1111/eva.12564>

440 Manel A, Holderegger R (2013) Ten years of landscape genetics. *Trends Ecol Evol* 28:614–621.
441 <https://doi.org/10.1016/j.tree.2013.05.012>

442 Mateo-Sánchez MC, Balkenhol N, Cushman S, et al (2015) A comparative framework to infer
443 landscape effects on population genetic structure: are habitat suitability models effective in
444 explaining gene flow? *Landsc Ecol* 30:1405–1420. <https://doi.org/10.1007/s10980-015-0194-4>

445 McRae BH (2006) Isolation By Resistance. *Evolution* 60:1551–1561. <https://doi.org/10.1554/05-321.1>

446 McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. *Proc*
447 *Natl Acad Sci U S A* 104:19885–19890. <https://doi.org/10.1073/pnas.0706568104>

448 Nagasaka A, Sugiyama S (2010) Factors affecting the summer maximum stream temperature of small
449 streams in northern Japan. *Bull Hokkaido For Res Inst* 47:35–43. (In Japanese with English
450 abstract)

451 Nakajima S, Sueyoshi M, Hirota SK, et al (2021) A strategic sampling design revealed the local
452 genetic structure of cold-water fluvial sculpin: a focus on groundwater-dependent water
453 temperature heterogeneity. *Heredity* 127:413–422. <https://doi.org/10.1038/s41437-021-00468-z>

454 Nakamura F (2022) Riparian forests and climate change: interactive zone of green and blue

455 infrastructure. In: Nakamura F (ed) Green Infrastructure and Climate Change Adaptation.
456 Springer, Singapore, pp 73–91

457 Nei M (1973) Analysis of gene diversity in subdivided populations. *Proc Natl Acad Sci U S A*
458 70:3321–3323. <https://doi.org/10.1073/pnas.70.12.3321>

459 Oksanen JF, Blanchet G, Friendly M et al (2019) vegan: community ecology package. R package
460 version 2.5-6. <https://CRAN.R-project.org/package=vegan>

461 Oliveira J dos A, Farias IP, Costa GC, Werneck FP (2019) Model-based riverscape genetics:
462 disentangling the roles of local and connectivity factors in shaping spatial genetic patterns of two
463 Amazonian turtles with different dispersal abilities. *Evol Ecol* 33:273–298.
464 <https://doi.org/10.1007/s10682-019-09973-4>

465 Paris JR, Stevens JR, Catchen JM (2017) Lost in parameter space: a road map for stacks. *Methods*
466 *Ecol Evol* 8:1360–1373. <https://doi.org/10.1111/2041-210X.12775>

467 Paz-Vinas I, Blanchet S (2015) Dendritic connectivity shapes spatial patterns of genetic diversity: A
468 simulation-based study. *J Evol Biol* 28:986–994. <https://doi.org/10.1111/jeb.12626>

469 Peakall R, Smouse PE (2012) GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for
470 teaching and research-an update. *Bioinformatics* 28:2537–2539.
471 <https://doi.org/10.1093/bioinformatics/bts460>

472 Peterson EE, Hanks EM, Hooten MB, et al (2019) Spatially structured statistical network models for
473 landscape genetics. *Ecol Monogr* 89:e01355. <https://doi.org/10.1002/ecm.1355>

474 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus
475 genotype data. *Genetics* 155:945–959. <https://doi.org/10.1093/genetics/155.2.945>

476 Rahel FJ, Keleher CJ, Anderson JL (1996) Potential habitat loss and population fragmentation for cold
477 water fish in the North Platte River drainage of the Rocky Mountains: Response to climate
478 warming. *Limnol Oceanogr* 41:1116–1123. <https://doi.org/10.4319/lo.1996.41.5.1116>

479 R Core Team (2019) R: a language and environment for statistical computing. R Foundation for
480 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

481 Sartor CC, Wan HY, Pereira JA, et al (2022) Landscape genetics outperforms habitat suitability in
482 predicting landscape resistance for congeneric cat species. *J Biogeogr* 49:2206–2217.

483 <https://doi.org/10.1111/jbi.14498>

484 Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in
485 landscape conservation planning: Comparison with existing indices and application to a case
486 study. *Landsc Urban Plan* 83:91–103. <https://doi.org/10.1016/j.landurbplan.2007.03.005>

487 Savary P, Foltête JC, Moal H, et al (2021) graph4lg: A package for constructing and analysing graphs
488 for landscape genetics in R. *Methods Ecol Evol* 12:539–547. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13530)
489 [210X.13530](https://doi.org/10.1111/2041-210X.13530)

490 Spear SF, Cushman SA, McRae BH (2015) Resistance Surface Modeling in Landscape Genetics. In:
491 Balkenhol N, Cushman SA, Storfer A, Waits LP (ed) *Landscape Genetics*. Wiley, New York, pp
492 129–148

493 Sugawara M (1979) Automatic calibration of the tank model. *Hydrological Sciences Bulletin* 24:375–
494 388. <https://doi.org/10.1080/02626667909491876>

495 Suyama Y, Hirota SK, Matsuo A, et al (2022) Complementary combination of multiplex high-
496 throughput DNA sequencing for molecular phylogeny. *Ecol Res* 37:171–181.
497 <https://doi.org/10.1111/1440-1703.12270>

498 Suyama Y, Matsuki Y (2015) MIG-seq: An effective PCR-based method for genome-wide single-
499 nucleotide polymorphism genotyping using the next-generation sequencing platform. *Sci Rep*
500 5:16963. <https://doi.org/10.1038/srep16963>

501 Suzuki H, Nakatsugawa M, Ishiyama N (2022) Climate change impacts on stream water temperatures
502 in the snowy cold region according to geological conditions. *Water* 14:2166.
503 <https://doi.org/10.3390/w14142166>

504 Suzuki K, Ishiyama N, Koizumi I, Nakamura F (2021) Combined effects of summer water
505 temperature and current velocity on the distribution of a cold-water-adapted sculpin (*Cottus*
506 *nozawae*). *Water* 13:975. <https://doi.org/10.3390/w13070975>

507 Ueda S, Nakatsugawa M, Usutani T (2020) Estimation of high-resolution downscaled climate
508 information based on verification of water balance in watershed of Hokkaido. *Journal of Japan*
509 *Society of Civil Engineers, Ser. B1 (Hydraulic Engineering)* 76:I_25–I_30.
510 https://doi.org/10.2208/jscejhe.76.2_I_25. (In Japanese with English abstract)

511 Wasserman TN, Cushman SA, Schwartz MK, Wallin DO (2010) Spatial scaling and multi-model
512 inference in landscape genetics: *Martes americana* in northern Idaho. *Landsc Ecol* 25:1601–
513 1612. <https://doi.org/10.1007/s10980-010-9525-7>

514 Wasserman TN, Cushman SA, Shirk AS, et al (2012) Simulating the effects of climate change on
515 population connectivity of American marten (*Martes americana*) in the northern Rocky
516 Mountains, USA. *Landsc Ecol* 27:211–225. <https://doi.org/10.1007/s10980-011-9653-8>

517 White SL, Hanks EM, Wagner T (2020) A novel quantitative framework for riverscape genetics. *Ecol*
518 *Appl* 30:e02147. <https://doi.org/10.1002/eap.2147>

519 Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: Impacts
520 across multiple levels of organization. *Philos Trans R Soc B Biol Sci* 365:2093–2106.
521 <https://doi.org/10.1098/rstb.2010.0055>

522 Wright S (1943) Isolation by distance. *Genetics* 28:114–138. <https://doi.org/10.1093/genetics/28.2.114>

523 Yagami T, Goto A (2000) Patchy distribution of a fluvial sculpin, *Cottus nozawae*, in the Gakko River
524 system at the southern margin of its native range. *Ichthyol Res* 47:277–286

525 Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a
526 review. *Landsc Ecol* 27:777–797. <https://doi.org/10.1007/s10980-012-9737-0>

527

528 **Statements & Declarations**

529 **Funding:** This study is partly supported by the research fund for the Ishikari and Tokachi Rivers
530 provided by the Ministry of Land, Infrastructure, Transport and Tourism of Japan.

531 **Competing Interests:** The authors declare no competing interests.

532 **Author Contributions:** Conceptualization, S.N. and F.N.; Data curation, S.N. and S.K.H.; Formal
533 analysis, S.N.; Funding acquisition; F.N.; Investigation, S.N., H.S., A.M., and S.K.H. ; Methodology,
534 S.N., H.S., M.N., and Y.S.; Project administration, F.N.; Resources, S.N., M.N., A.M., and Y.S.;
535 Software, S.N. and H.S., A.M., and S.K.H.; Supervision, M.N., Y.S. and F.N.; Validation, S.N. and
536 F.N.; Visualization, S.N.; Writing – original draft, S.N. and H.S. ; Writing – review & editing, S.N.,
537 H.S., M.N., A.M., S.K.H., Y.S., and F.N.

538 **Data Availability:** Genetic and environmental data generated in this study were deposited at Figshare

539 (doi: 10.6084/m9.figshare.19694989).

540

541 **Table 1** Riverscape variables considered in the present study.

Variable	Description	Hypothesis / Ecological importance	Ranges
Summer water temperature ^A	Mean water temperature from July to August (July 2019 to August 2019) [°C]	Streams with low summer water temperatures are suitable for <i>C. nozawae</i> occupancy/survival (Yagami and Goto 2000; Suzuki et al. 2021) and therefore migration may also occur frequently in these streams.	8.32–14.2
Water temperature fluctuation ^A	Standard deviation of the water temperature in one year (September 2018 to August 2019)	Thermally stable streams can be suitable for migration.	1.97–5.09
Drought water discharge ^{BC}	Flow rate on the day when the flow is 355th highest in one year [m ³ /s] (September 2018 to August 2019)	Drought water discharges, which particularly reflect the environmental heterogeneity created by groundwater (Nagasaka and Sugiyama 2010), ensure opportunities to colonize throughout the year.	0.07–6.24
Flow fluctuation ^{AB}	Coefficient of variation in the daily flow rate in one year (September 2018 to August 2019)	Hydrologically stable streams can be suitable for migration.	0.31–0.65
Edge length	Length of edges [km]	Isolation by distance (Wright 1943)	0.05–7.19
Slope	Mean gradient of the edge, i.e., the elevation range divided by edge length	Fish movement and migration are often impeded on steep slopes (Kanno et al. 2011).	4.15–56.5
Strahler's stream order ^C	Strahler's stream order of the edge	Even in cold-water fish, the mainstem may function as a corridor that facilitates connectivity among populations (White et al. 2020).	1–4
Shreve's stream order ^{BC}	Shreve's stream order (link magnitude), i.e., the numbers of confluence points upstream, at the midpoint of the edge	Given the dendritic arrangement and asymmetry of stream networks, sections with more confluence points upstream may increase the number of migrants passing through (Paz-Vinas and Blanchet 2015).	1–62
Catchment area ^{BC}	Cumulative area of the catchment calculated at the midpoint of the edge [km ²]	Sections with larger catchment areas may have more migrants passing through, based on the same principle as that of the stream order. Or, conversely, streams with larger catchment areas have been identified to have lower <i>C. nozawae</i> occupancies (Suzuki et al. 2021) and therefore it is also possible that less migration occurs in sections with larger catchment areas.	6.4–296.3
Direction	Whether the gene flow is toward the upstream (0) or downstream (1) direction	Most stream organisms have higher migration rates in the downstream direction than in the upstream direction (Lamphere and Blum 2012).	0 or 1

542 Variables with the same letters (A, B, C) have high correlations ($|r| > 0.7$); these variables were not included in the same model.

543 **Table 2** Selected models explaining the strength of gene flow on the edges. Estimated β values
 544 (median) and their 95% credible intervals (95% CI) are displayed.

Variables	β	95% CI
(A) G_{ST}		
(Intercept)	5.84	5.65, 5.98
Shreve's stream order	4.51	3.96, 5.19
Water temperature fluctuation	-0.48	-0.61, -0.35
Slope	-0.94	-1.15, -0.67
Edge length	-0.42	-0.54, -0.32
(B) D_{PS}		
(Intercept)	6.06	4.94, 6.85
Strahler's stream order	2.50	1.72, 3.15
Summer water temperature	-1.42	-2.49, -0.38

545

546 **Figure Legends**

547 **Fig. 1** Location of the study area. The blue network indicates the rivers belonging to the Ishikari River
 548 system, which has the second largest watershed in Japan and includes the Sorachi River.

549

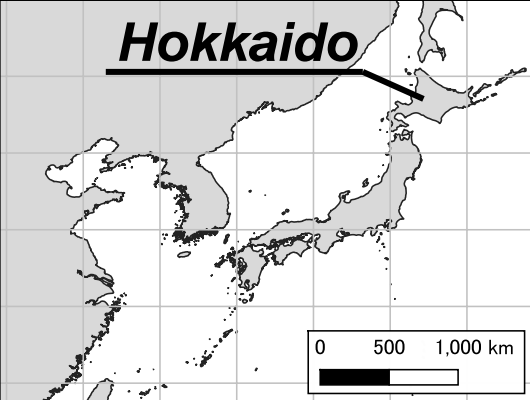
550 **Fig. 2** Maps of the Sorachi River watershed showing the study area (a) and landscape resistance
 551 estimated by BGR models (b–d). In panel (a), sampling nodes (sampling sites) and unsampled nodes
 552 (major confluences between them), which are delimitations of edges (stream sections), are denoted.
 553 Barplots with each sampling node indicate the population structure inferred by STRUCTURE ($K = 6$).
 554 Landscape resistance is shown in three patterns: long-term gene flow modeled by G_{ST} (b), recent gene
 555 flow modeled by D_{PS} (c), predicted gene flow at the end of the 21st century derived by substituting
 556 future water temperatures into the model derived by D_{PS} (d).

557

558 **Fig. 3** Isolation by distance and isolation by resistance. The relationship between pairwise genetic
 559 distance and cumulative landscape resistance between populations (b, d) is compared to the
 560 relationship with simple waterway geographic distance (a, c). The cases of G_{ST} (a, b) and D_{PS} (c, d) are
 561 shown.

562

Hokkaido



145°

45°

Sea of Okhotsk

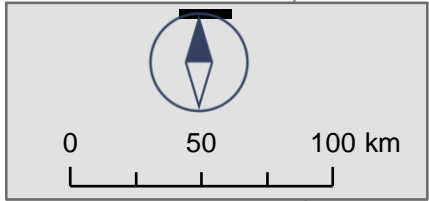
140°

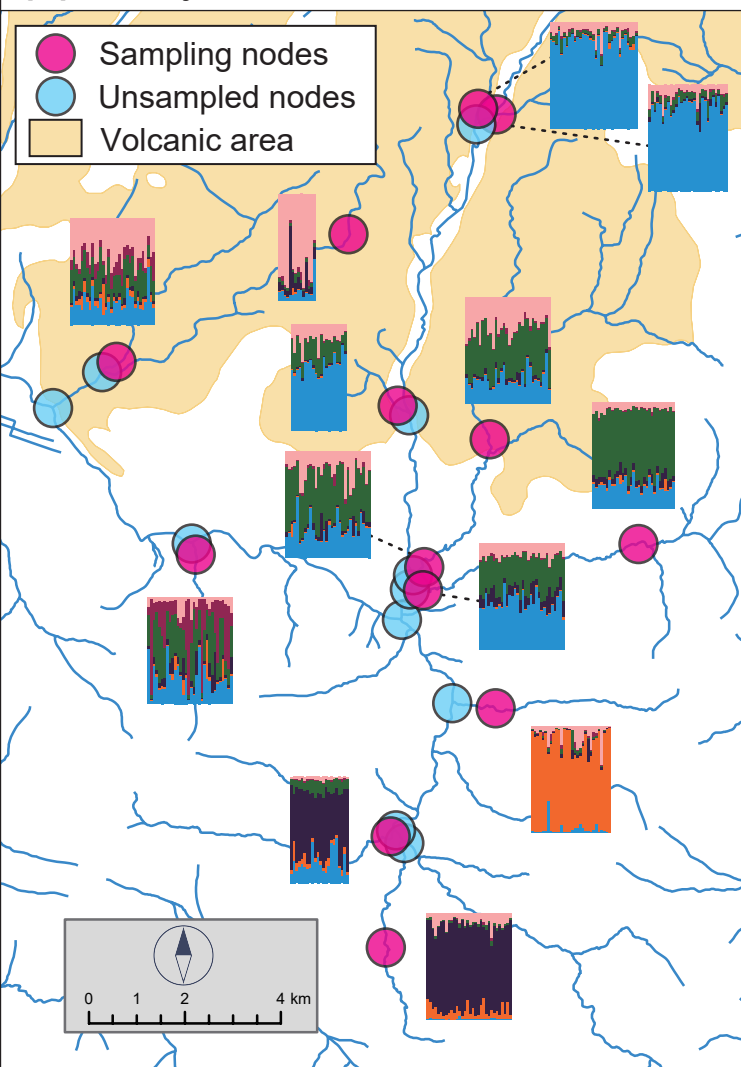
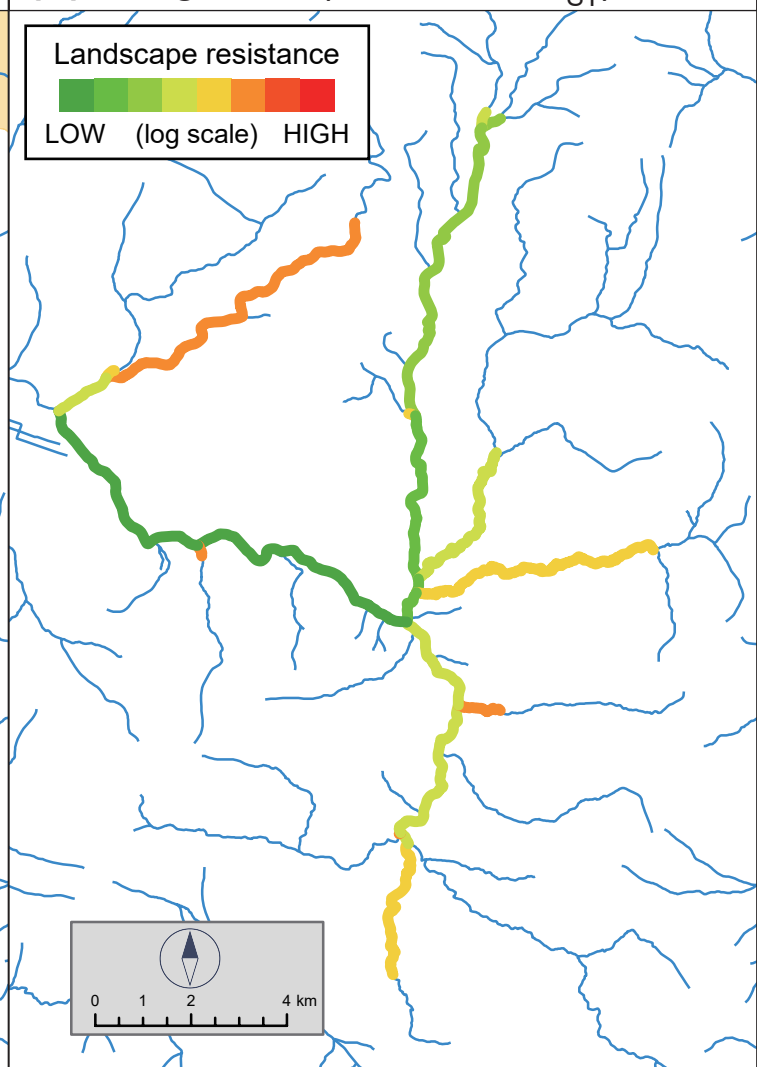
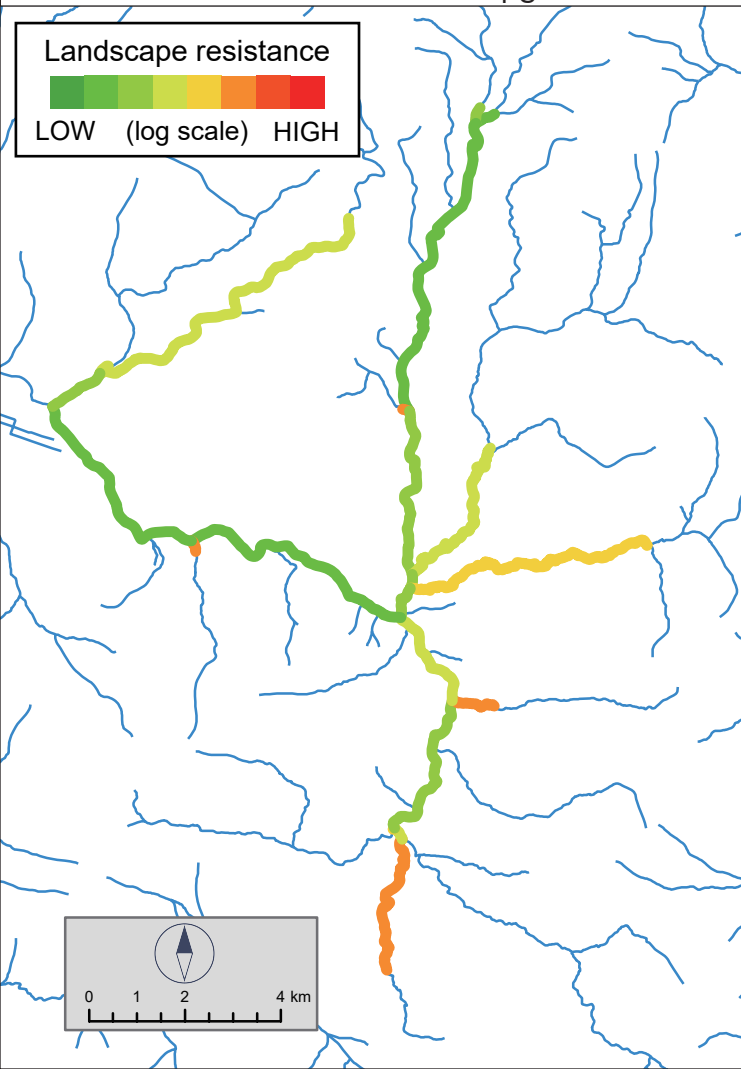
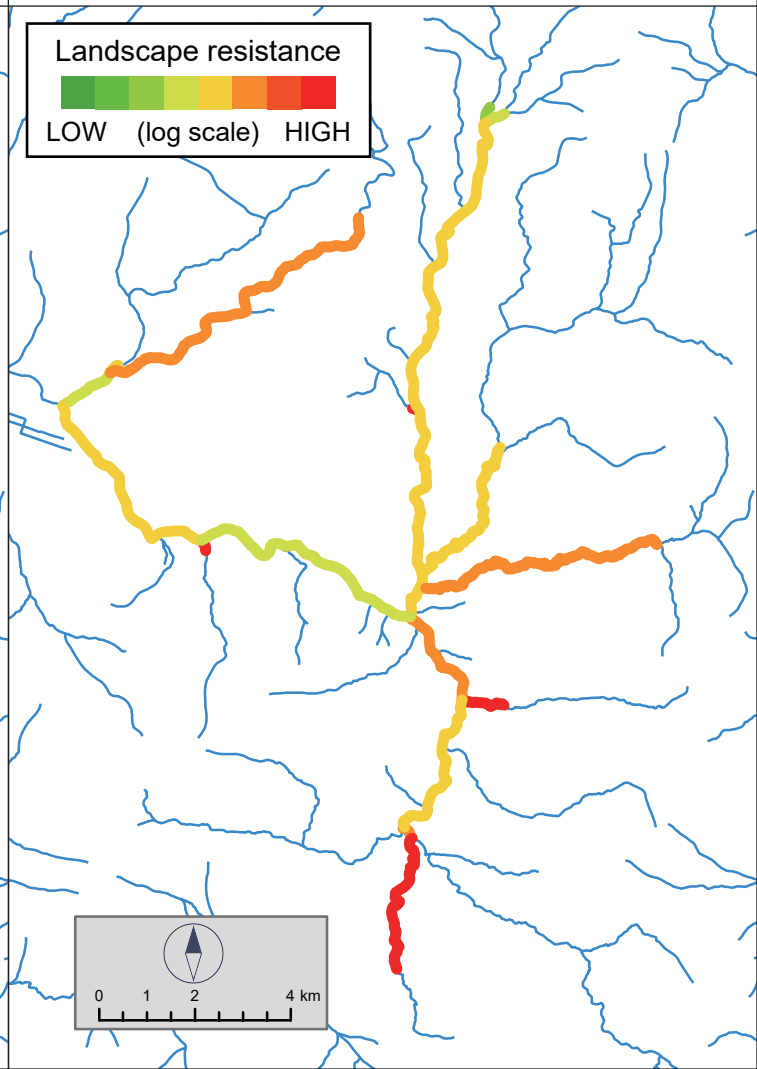
Sea of Japan

Study area

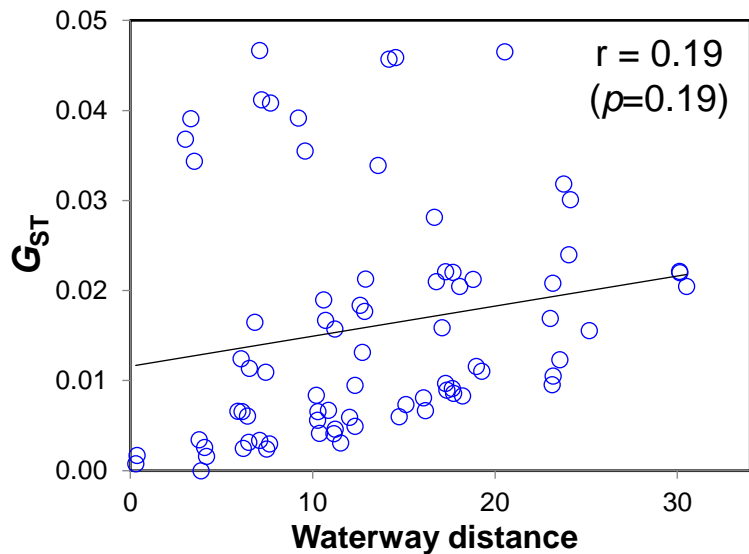
Lake Kanayama

Pacific Ocean

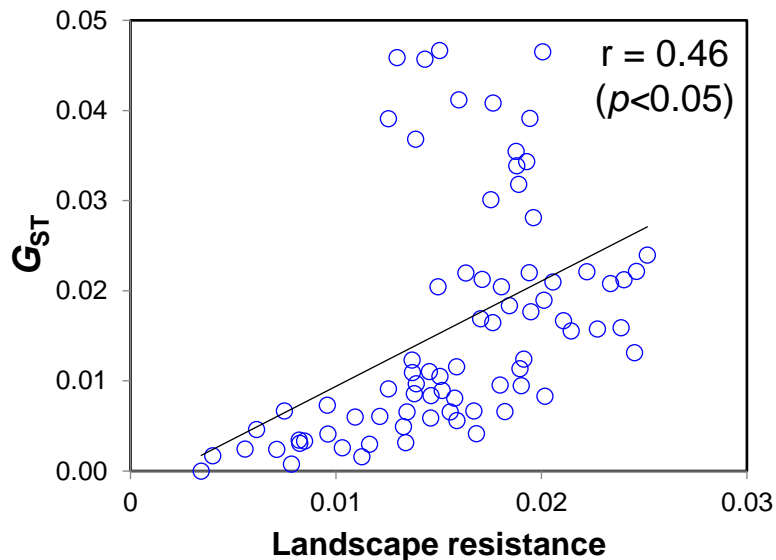


(a) Study sites**(b) Long-term (based on G_{ST})****(c) Current (based on D_{PS})****(d) Future (at the end of 21C)**

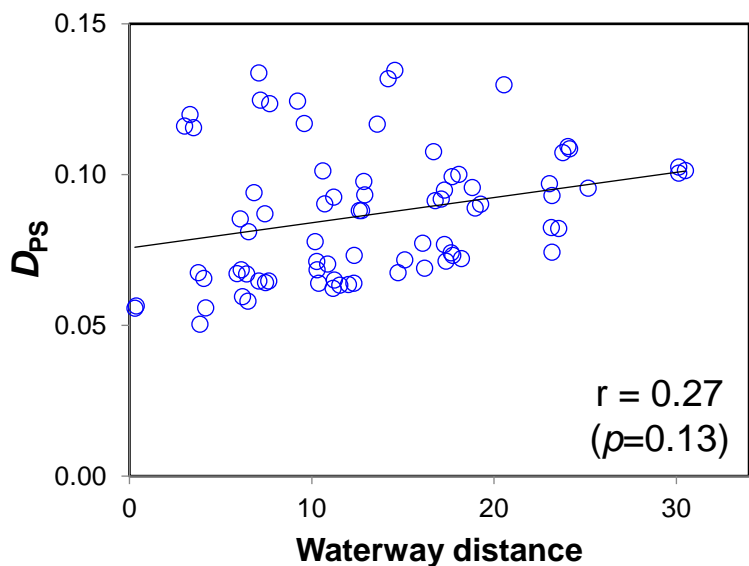
(a) G_{ST} - Isolation by distance



(b) G_{ST} - Isolation by resistance



(c) D_{PS} - Isolation by distance



(d) D_{PS} - Isolation by resistance

