

Historical connectivity but contemporary isolation: genetic diversity, gene flow, and conservation units in *Myricaria germanica* in Central Europe

Tania Chavarria

tchavarria@uni-muenster.de

Systematics and Ecology of Fungi and Algae

Silke werth

Systematics and Ecology of Fungi and Algae

Kailin Weitkämper

Systematics and Ecology of Fungi and Algae

Christoph Scheidegger

Swiss Federal Research Institute WSL

Research Article

Keywords:

DOI: <https://doi.org/>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

1 Historical connectivity but contemporary isolation: genetic diversity, gene flow, and
2 conservation units in *Myricaria germanica* in Central Europe

3
4 Tania Chavarria-Pizarro^{1,2}, Christoph Scheidegger³, Kailin Weitkämper¹, Silke
5 Werth^{1,3}
6

7 1 Systematics and Ecology of Fungi and Algae, LMU Munich, Germany

8 2 Current address: Molecular Evolution and Sociobiology Group, Institute for
9 Evolution & Biodiversity University of Münster, Germany

10 3 Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

11 *to whom correspondence should be sent: tchavarria@uni-muenster.de,
12 werth@bio.lmu.de
13

14 **Abstract**

15 Habitat fragmentation and the disruption of river connectivity threaten the long-term
16 persistence of riparian species by reducing gene flow, increasing inbreeding, and
17 eroding genetic diversity. *Myricaria germanica*, a pioneer shrub once widespread
18 throughout European river systems but now largely confined to fragmented
19 headwater populations, provides an excellent model for investigating how historical
20 and contemporary processes shape genetic diversity and connectivity in threatened
21 riparian plants. We analyzed genetic diversity, population structure, and migration
22 across 67 populations from 12 Central European river catchments using 20 nuclear
23 and six chloroplast microsatellite loci, enabling comparisons of pollen- and seed-
24 mediated gene flow across contemporary and historical timescales. Both marker
25 systems revealed low genetic diversity, high inbreeding, and strong population
26 differentiation, indicating pronounced genetic subdivision throughout the species'
27 range. Gene flow was highly asymmetric among catchments, with the Tagliamento

acting as a major genetic sink, the Rhine serving as a regional connectivity hub, and the Po exhibiting more balanced genetic exchange. Nuclear markers revealed widespread and relatively symmetrical gene flow, consistent with extensive pollen-mediated connectivity and historical long-distance seed dispersal, whereas chloroplast markers showed limited and directional gene flow, reflecting restricted seed dispersal. Contemporary migration analyses further indicated that seed-mediated gene flow is now largely confined within individual catchments despite evidence of broader historical connectivity. Together, these findings support a two-phase postglacial colonization scenario involving rare long-distance seed dispersal during range expansion, followed by prolonged pollen-mediated gene flow. The marked genetic differentiation among catchments and the limited contemporary dispersal indicate that individual river catchments represent biologically meaningful conservation units that harbor unique components of the species' genetic diversity. Overall, our results demonstrate that *M. germanica* retains clear signatures of historical connectivity but is undergoing increasing contemporary genetic isolation. These findings underscore the importance of maintaining river connectivity, prioritizing genetically important catchments such as the Rhine and Tagliamento, and preserving the evolutionary potential of this threatened riparian species.

1 Introduction

Myricaria germanica Desv. is a threatened riparian pioneer shrub specialized on open gravel bars within the active flood zones of rivers, where periodic disturbance and adequate water availability create suitable conditions for seed germination and establishment (Werth et al. 2014; Sitzia et al. 2021). Although the genus *Myricaria* Desv. is widely distributed across Eurasia and most likely originated

in the Qinghai–Tibetan Plateau region (Sun & Werth 2024), *M. germanica* is its only European representative (Webb 1968). Once widespread throughout the upper and middle reaches of European river systems, the species has undergone severe range contraction and now persists primarily as fragmented populations in headwater catchments that retain relatively natural fluvial dynamics (Werth et al. 2014; Gostner et al. 2017). This decline has been driven largely by river regulation, including dam construction, channelization, embankment development, and flood-control measures, which disrupt sediment transport, reduce the formation of pioneer gravel habitats, and diminish connectivity among populations (Jansson et al. 2000; Werth et al. 2014; Lind et al. 2019; Fink et al. 2022; Weitkämper et al. 2026). These alterations have transformed formerly connected river networks into increasingly fragmented landscapes, raising concerns about the long-term persistence and evolutionary resilience of riparian species.

The conservation importance of *M. germanica* is formally recognized in European environmental policy. It is the characteristic species of the Natura 2000 habitat "Alpine rivers and their ligneous vegetation with *Myricaria germanica*" (habitat code 3230) under the European Union Habitats Directive (European Environment Agency 2013) and an indicator species of the habitat "Sparsely vegetated river gravel banks" (habitat code C3.55) in the *Interpretation Manual of the Habitats Listed in Resolution No. 4 (1996)* (Evans & Roekaerts 2019). As an indicator species, its occurrence reflects the ecological integrity of dynamic alpine river ecosystems, while its role in supporting diverse insect and bird communities identifies it as a keystone species within European riparian habitats (Kudrnovsky & Stöhr 2013). Consequently, conserving the remaining populations of *M. germanica* is important not only to prevent further local extinctions and genetic erosion, but also to preserve the

biodiversity, ecological functioning, and natural dynamics of European river ecosystems.

Habitat fragmentation alters evolutionary processes by reducing gene flow, increasing genetic drift and inbreeding, and ultimately eroding the adaptive potential and long-term viability of natural populations. Consequently, understanding how genetic diversity and connectivity are maintained across fragmented landscapes is a central objective of conservation genetics because genetic diversity provides the evolutionary basis for adaptation and population persistence under environmental change (Hedrick 2005; Lee & Mitchell-Olds 2011; Meirmans 2012; Wang & Bradburd 2014; Tian et al. 2020). Population genetic analyses of diversity, inbreeding, population structure, and gene flow can reveal the extent to which habitat fragmentation has disrupted connectivity and provide the information required to identify conservation units and prioritize management actions (Hedrick 2005; Meirmans 2012; Wang & Bradburd 2014). *Myricaria germanica* therefore represents an excellent model for investigating the genetic consequences of river regulation and habitat fragmentation in riparian ecosystems, where dispersal is strongly constrained by the dendritic structure of river networks (Werth et al. 2014; Lind et al. 2019; Fink et al. 2022).

Contemporary patterns of genetic diversity, however, reflect not only recent habitat fragmentation but also historical demographic processes. Quaternary climatic oscillations profoundly reshaped the distribution of European biota, with species persisting in multiple glacial refugia before recolonizing newly available habitats following ice retreat (Dansgaard et al. 1993; van Andel & Tzedakis 1996; Birks & Ammann 2000; Taberlet et al. 1998; Petit et al. 2003; Hewitt 2004; Petit et al. 2005b; Schönswetter et al. 2005). In mountain systems, many plant species additionally

survived in ice-free refugia within the Alps (Parisod 2022). Because *M. germanica* occupies riparian habitats spanning glacier forefields to lowland river systems (Sitzia et al. 2021), both postglacial recolonization and recent anthropogenic fragmentation are likely to have contributed to its contemporary genetic structure. Distinguishing the relative influence of these historical and contemporary processes is therefore essential for understanding patterns of genetic variation and developing effective conservation strategies for threatened riparian species (Petit et al. 2005; Werth et al. 2014; Tian et al. 2020).

Dispersal in riparian plants is inherently asymmetric because pollen and seeds are transported by different vectors operating across contrasting spatial and temporal scales. Pollen, dispersed primarily by wind or insects, can facilitate gene flow over considerable distances and even across watershed boundaries, reducing genetic differentiation in biparentally inherited nuclear genomes (Ennos 1994; Petit et al. 2005). In contrast, seed dispersal is largely constrained by river networks, occurring predominantly through hydrochory along river corridors and exhibiting strong downstream directionality despite occasional long-distance dispersal events (Nilsson et al. 2010; Werth et al. 2014; Auffret et al. 2015). Consequently, maternally inherited chloroplast genomes often exhibit stronger spatial genetic structure than nuclear genomes because they primarily reflect seed dispersal and historical colonization pathways rather than contemporary pollen movement (Petit et al. 2005; Zhang & Hewitt 2003). In several riparian pioneer species, including *M. germanica*, *Populus nigra*, and *Salix* spp., seeds are dispersed by both wind and water, although hydrochory generally dominates and promotes downstream gene flow (Imbert et al. 2003; Liu et al. 2006; Honnay et al. 2010; Kikuchi et al. 2011; Love et al. 2013; Fink et al. 2017). Because *M. germanica* combines selfing with anemochorous and

hydrochorous seed dispersal, effective seed-mediated gene flow is expected to occur primarily over local spatial scales, whereas pollen dispersal may maintain genetic connectivity among otherwise isolated populations (Fink et al. 2017). Comparing pollen- and seed-mediated dispersal therefore provides a powerful framework for disentangling historical and contemporary connectivity and evaluating how habitat fragmentation has affected different components of gene flow.

Nuclear and chloroplast microsatellites provide complementary insights into population connectivity because they differ in inheritance and evolutionary dynamics. Biparentally inherited nuclear microsatellites are widely used to quantify genetic diversity, population structure, and contemporary gene flow owing to their high mutation rates and reproducibility (Morgante & Olivieri 1993; Streiff et al. 1999; Jones & Ardren 2003; Patreze & Tsai 2010; Perdereau et al. 2014). In contrast, maternally inherited chloroplast microsatellites in angiosperms primarily trace seed-mediated dispersal and historical demographic processes because of their lower evolutionary rates and greater conservation across taxa (Provan et al. 1998; Streiff et al. 1999; Grivet et al. 2006; Petit et al. 2005; Papi et al. 2012). Integrating both marker systems therefore provides a powerful framework for disentangling the relative contributions of pollen- and seed-mediated gene flow, reconstructing postglacial recolonization, and assessing the extent to which contemporary connectivity persists among fragmented river catchments (Djedid et al. 2022).

The aim of this study was to investigate genetic diversity, population structure, and connectivity in *Myricaria germanica* across the major river catchments of Central Europe using complementary nuclear and chloroplast microsatellite markers. By jointly analysing biparentally inherited nuclear and maternally inherited chloroplast genomes, we compared pollen- and seed-mediated gene flow across both

contemporary and historical timescales. Specifically, we aimed to (i) quantify genetic diversity and inbreeding within and among river catchments; (ii) characterize population genetic structure across the Central European distribution of *M. germanica*; and (iii) evaluate historical and contemporary patterns of pollen- and seed-mediated connectivity. To our knowledge, this represents the most comprehensive comparative assessment of nuclear and chloroplast genetic variation across the Central European range of *M. germanica*. By integrating historical and contemporary perspectives on gene flow, our study provides new insights into the genetic consequences of river regulation and habitat fragmentation and identifies biologically meaningful conservation units to support the long-term management of this threatened riparian species.

2 Materials and methods

2.1 Sampling

Our sampling included 2178 individuals of the riparian shrub *Myricaria germanica* collected from 67 populations, situated in 12 catchments of rivers in Central and Eastern Europe (Table 1, Fig 1). The sampling strategy followed Werth and Scheidegger (2014), and a part of the populations included in this previous study were reanalysed for the present study. The number of sampling sites reflected the population number of the species in each catchment. For sampling, we used apical tips of branches without flowers, to avoid including seeds or pollen deposited on the plants. Samples were stored on silica gel at room temperature until DNA extraction. In large populations, tissue was sampled from 40 adult plants along a transect through the population following the flowing direction of the river, keeping at least 2m between adjacent plants. In small populations, tissue was collected from all plants.

For each population, GPS coordinates were recorded of the sampled specimens, and the local population size was estimated. In small populations, the plants were counted. In large populations, the individuals occupying a part of the area were counted and this number was used for extrapolation to the total area; those latter estimates were provided as intervals.

Collecting permits were obtained from regional authorities when samples were collected in protected areas, but mostly we collected from public not protected areas.

2.2 Genetic data and microsatellite methods

DNA was extracted with the DNeasy 96 plant kit (Qiagen). PCR, fragment analyses, and genotyping of 20 nuclear and six chloroplast microsatellites were performed according to the description in Werth and Scheidegger (2011) but leaving out the microsatellite loci Mg461 and Mg482 which proved difficult to amplify and had many missing genotypes.

2.3 Genotypic analysis

2.3.1 Levels of genetic diversity

As measures of genetic variability within populations, the mean number of alleles (N_a), effective alleles number (N_e), the Shannon index (I), observed heterozygosity (H_o), and expected heterozygosity (H_e) were calculated using the R package 'adeigenet' (adeigenet_2.1.10) (Jombart & Ahmed 2011). Furthermore, Nei's gene diversity (H), allelic richness (A_R), and inbreeding coefficient (F_{IS}) within populations were computed using the 'hierfstat' R package version 0.5-11 (Nei 1973, Goudet et al. 2002). For each locus, deviation from Hardy–Weinberg equilibrium (HWE) was tested, using Fisher's exact tests implemented in adegenet (Jombart & Ahmed 2011). A heatmap was created to visualize HWE for each locus per population for nuclear data using R version 4.5 (R Core Team 2019).

2.3.2 Genetic structure and population differentiation

The population genetic variance for both types of microsatellites (nuclear and chloroplast) was analyzed in GenoDive (version 3.0) (Meirmans 2020), which offers robust and flexible functional analysis of haploid datasets, treating them with the same precision and adaptability afforded to diploid and polyploid data. GenoDive allows the application of comprehensive statistical analyses across ploidy levels and efficient multithreaded processing, making it especially well-suited for handling mitochondrial, chloroplast, or other types of haploid genetic data (Meirmans 2020). With GenoDive, we calculated a global analysis of molecular variance (AMOVA), average F -statistics, pairwise fixation indices (F_{ST}), and their significance levels (p -values) which were estimated with 1,000 permutations (Excoffier et al. 2005, Weir & Cockerham 1984). For chloroplast data, we calculated Φ_{ST} (PhiST), which is the proportion of total genetic variance that is due to differences among populations based on genetic distances between genotypes, according to the formula below:

$$\Phi_{ST} = \frac{\sigma_{among\ populations}^2}{\sigma_{total}^2}$$

Separate heatmaps were created to visualize all pairwise F_{ST} and Φ_{ST} values between the *M. germanica* populations for the nuclear and chloroplast microsatellites respectively.

Next, we tested for isolation by distance by regressing pairwise genetic distance i.e. linearized $F_{ST} = [F_{ST} / (1 - F_{ST})]$, against the decadic logarithm of geographical distance [km] across populations for the nuclear data (for chloroplast Φ_{ST}) and used a Mantel test (Mantel 1967) with 1,000 permutations implemented in the 'adeigenet' package to determine if there was a correlation between genetic and geographic distance.

Population structure was assessed using Bayesian model-based clustering implemented in STRUCTURE version 2.3.4 assuming admixed ancestry and correlated allele frequencies (Pritchard, Stephens & Falush 2007). Twenty independent runs were performed for each K value, the number of genetic clusters, which ranged from 1 to 12 which where the number of catchments (the likelihood rapidly declined with increasing K values in preliminary runs after K=2). As further parameters, a burn-in period of 50,000 iterations and 1,000,000 Markov Chain Monte Carlo (MCMC) replicates were used. The most likely number of genetic clusters K was determined by considering the log-likelihood of each K value and using the ΔK method described by Evanno, Regnaut, and Goudet (2005), which was implemented in Structure Harvester (Earl & von Holdt 2012). The ΔK graph exhibits a maximum at the most likely value of K. These analyses allowed the detection of two distinct clusters with high admixture (see Results). Because it is known that in the presence of a major grouping, STRUCTURE will not be able to detect finer structuring (Pritchard, Stephens & Falush 2007), we ran separate STRUCTURE analyses with each of the river catchments to identify subgroups. In these new analyses, we again considered K between 1 and 12.

Discriminant Analysis of Principal Components (DAPC) was used to further pinpoint subpopulations of the species, using the 'adeigenet' package in R (Jombart & Ahmed 2011, R Core Team 2019). The number of clusters was assessed using the function 'find.clusters', evaluating a range from 1 to 12. The optimal number of clusters was identified based on the Bayesian information criterion (BIC), as suggested by Jombart & Ahmed (2011). The function 'find.clusters' was used to transform original data into principal components (PCs), retaining 50 PCs in the analysis. The DAPC function performed a discriminant analysis using 10 PCs (>80%

of variance explained), and ten eigenvalues were retained and examined. Ten independent runs were executed, and the average results were plotted. We performed all the genetic structure analyses for all the 67 populations independently first. Then, we grouped the populations by the catchment that they belonged to and performed the genetic structure analysis on those 12 catchments (Fig 1, Table 1). In addition, we constructed phylogenetic trees for nuclear and chloroplast data using neighbor-joining (NJ) and Unweighted Pair Group Method with Arithmetic Mean (UPGMA) methods in R with phangorn (Schliep 2011) and ape (Paradis et al. 2004). We used 5,000 bootstraps using the function “bootstrap.phyDat”.

As we said above, the analysis of molecular variance was calculated using the software GenoDive the same we used to estimate the F-statistics (Weir and Cockerham, 1984). AMOVA and associated significance levels (p-values) were estimated using 1,000 permutations (Excoffier et al. 2005; Weir & Cockerham 1984). Variance components obtained from the AMOVA were subsequently used to estimate the relative contributions of pollen- and seed-mediated gene flow to total gene flow, applying the approach described by Ennos (1994):

$$(Pollen\ flow)/(Seed\ flow) = ((1/\Phi_{SC}(B) - 1)/(1/\Phi_{SC}(M) - 1)) - 1$$

Where are $\Phi_{SC}(B)$ and $\Phi_{SC}(M)$ levels of population differentiation calculated from biparentally (nuclear) and maternally (cpDNA) inherited markers, respectively. The calculation of the pollen–seed flow ratio presented here assumes that maternal inheritance of cpDNA is the rule in *M. germanica*, as in most other angiosperms (Ennos et al. 1999).

2.3.2 Migration levels

276 Next, we tested specific models about the directionality of gene flow and to computed
277 Bayesian estimates of effective population sizes and bidirectional rates of migration
278 in *M. germanica*. This analysis was performed using nine of the 12 river catchments.
279 We excluded from the analysis all catchments that only contained data from one
280 single population (Oder, Danube and Aare) as these had a different geographic
281 extent of sampling than the remaining catchments. We used the coalescent-based
282 software MIGRATE-n version 3.26 (Beerli & Felsenstein 2001; Beerli 2016) for
283 nuclear (diploid) and chloroplast data (haploid). MIGRATE-n makes the following
284 assumptions: i) constant population size through time or random fluctuation around
285 an average size; ii) individuals are randomly mating within populations; iii) the
286 mutation rate is constant through time and is the same in all parts of the genealogy;
287 iv) the immigration rate is constant through time; and v) the studied populations
288 exhibit a recent divergence and not an old split, so they exchange material through
289 gene flow. We ran MIGRATE-n to estimate migration rates among catchments (all
290 parameters free to vary) with one long MCMC chain, sampling every 1,000th step for
291 a total of 200,000,000 genealogies after a burn-in of 200,000 steps in the chain. A
292 Brownian motion model was used, which approximates the stepwise mutation model
293 commonly used for microsatellite data but converges faster. The populations from
294 each catchment were randomly resampled to 100 individuals to speed up
295 convergence. Starting parameters for population size h and migration rates were
296 inferred from F_{ST} values, mutation rate modifiers were deduced from the data using
297 Watterson's h . We performed a series of preliminary runs to explore run conditions
298 and prior distributions for the data from each catchment. Bayesian estimation of
299 migration rate and population sizes were run with one long chain and static heating
300 (temperatures of four Markov chains: 1, 1.5, 3, 10,000,000). To facilitate comparisons

among migration pathways, we converted posterior median mutation-scaled migration rates (M) into relative migration probabilities scaled between 0 and 1. These probabilities represent the proportion of total inferred gene flow attributed to each migration route. For every directed migration parameter $M_{j \rightarrow i}$, relative migration probability $P \in [0, 1]$ is:

$$P_{j \rightarrow i} = \frac{M_{\text{median. } j \rightarrow i}}{\sum_{\text{all pairs}} M_{\text{median}}}$$

As we found that seed likely dominates over pollen dispersal in *M. germanica* contemporary migration patterns (see results), we calculated the recent migration rates between the 12 catchments with the nuclear microsatellite data by implementing BA3-MSAT from BayesAss version 3.0.5 (Wilson & Rannala 2003) and compared them with the relative migration rates obtain for the nuclear data with MIGRATE-n. First, we assessed the optimal mixing parameters for migration rates ($\delta M = 0.1$), allele frequencies ($\delta = 0.55$), and inbreeding coefficients ($\delta F = 0.0375$) by running ten repetitions in BA3-MSAT-autotune version 3.0.5 as recommended by Musssmann et al. (2019). Subsequently, BA3-MSAT was run with the predefined mixing parameters for 50 million generations, sampling every 100th generation. The first million generations were discarded as burn-in and chain convergence was assessed in Tracer version 1.7.1 (Rambaut et al. 2018).

3 Results

3.1 Genetic diversity

Across the 20 nuclear microsatellite loci, we detected a total of 169 alleles, with low to moderate null allele frequencies (0.023–0.17). As null allele frequencies were low, no loci were excluded from subsequent analyses. In total, 1,684 multilocus genotypes (MLGs) were identified. The number of alleles per locus ranged from three to 22,

expected heterozygosity (H_s) ranged from 0.06 to 0.40, and F-statistics indicated substantial genetic structure ($F_{IS} = 0.24\text{--}0.47$; $F_{IT} = 0.36\text{--}0.81$; $F_{ST} = 0.35\text{--}0.80$; Table S1). At the population level, the number of MLGs ranged from two to ten. Shannon diversity indices ranged from 0 to 0.99, while Nei's gene diversity varied between 0 and 0.50 (Table 2). Inbreeding coefficients (F_{IS}) were high across populations (0.10–0.93), and population-level F_{ST} values ranged from 0.36 to 0.95 (Fig. S1A). Most populations showed high levels of homozygotes at multiple loci according to the Hardy–Weinberg equilibrium ($p < 0.05$; Fig. S2). Using six haploid chloroplast microsatellite loci, we detected 30 alleles and identified 55 chloroplast multilocus genotypes. The number of alleles per locus ranged from two to nine (Table S2). Estimates of population structure were high (Φ_{ST} ($PhiST$) = 0.10–0.44; Table S2), and Shannon diversity indices varied from 0 to 0.94 (Table 3).

3.2 Population genetic structure

3.2.1 Nuclear microsatellites

Bayesian clustering analysis of nuclear microsatellites (STRUCTURE) identified two main genetic clusters ($K = 2$; Fig. 2A–B, Fig. 3). Most populations were dominated by a single cluster, although several showed varying degrees of admixture (Fig. 2A; Figs. S3–S15). Given the large dataset (67 populations, 2,212 individuals). STRUCTURE and DAPC analyses were also conducted separately for each of the 12 river catchments (Table 1). In most cases, catchment-level analyses revealed patterns consistent with the global $K = 2$ structure (Figs. S3–S15). Pairwise nuclear F_{ST} values were moderate to high and increased with geographic distance. Populations separated by large distances (e.g. relative to CZE1 and UKR1) expectedly showed very high differentiation ($F_{ST} = 0.75\text{--}0.95$; Fig. S1A). Isolation by

distance was tested using a Mantel test, comparing pairwise genetic and geographic distances. We detected a significant positive relationship between genetic and geographic distance based on nuclear microsatellites (Mantel's $r = 0.37$, $p = 0.00001$), indicating that geographic distance acts as a barrier to gene flow among populations (Fig. S16). Analysis of molecular variance (AMOVA) attributed 49% of the total variation to differences among populations and 51% to differences among individuals within populations ($p < 0.05$; Table S3).

3.2.2 Chloroplast microsatellites

STRUCTURE analysis of chloroplast microsatellites also supported two main genetic clusters ($K = 2$; Fig. 5A–B; Fig. S17), largely concordant with the nuclear results. However, chloroplast data showed substantially lower admixture, with most populations dominated by a single cluster (Fig. 5A). Pairwise chloroplast F_{ST} values were moderate to high and increased with geographic distance (Fig. S1B), indicating stronger population structure than observed for nuclear markers. DAPC based on chloroplast microsatellites revealed clearer spatial separation among populations compared to nuclear data (Fig. 5B). For chloroplast microsatellites, isolation by distance was weaker but still significant (Mantel's $r = 0.22$, $p = 0.001$), suggesting more complex or historically contingent patterns of seed-mediated dispersal. AMOVA based on chloroplast microsatellite haplotypes revealed strong population structure, with 75.25% of the genetic variation occurring among populations and 24.75% within populations ($\Phi_{ST} \approx 0.75$, $p < 0.01$), consistent with highly restricted seed-mediated gene flow.

3.3 Genetic structure and dispersal among catchments

3.3.1 Nuclear and chloroplast structure among catchments

DAPC of nuclear microsatellites showed that the first two discriminant axes explained 33.7% of the total genetic variance (Fig. 4A). Individuals grouped into three main clusters: a central cluster containing individuals from most catchments, a second cluster dominated by individuals from the Isar and Lech catchments, and a third cluster comprising individuals from Tagliamento and subsets of Po and Drau. Clusters two and three were more closely related to each other than to the central group, as reflected by their proximity in the UPGMA tree (Fig. 4B). Populations within the same catchment generally exhibited lower differentiation; however, several cases of high within-catchment F_{ST} were observed (Fig. S1A; Figs. S3–S15). Notably, populations exhibiting strong genetic differentiation also showed high inbreeding coefficients, but were not consistently more geographically isolated than other populations within the same catchment (Table 2). Analysis of molecular variance (AMOVA) among catchments ($n=12$) revealed strong and significant genetic structuring among populations. A total of 36.7% of the genetic variation was attributable to differences among populations ($F_{ST} = 0.367$, 95% CI: 0.332–0.399, $p = 0.001$), while 37.0% of the variation occurred among individuals within populations ($F_{IS} = 0.584$, 95% CI: 0.553–0.620, $p = 0.001$). Only 26.3% of the variation was found within individuals ($F_{IT} = 0.737$). These results indicate pronounced differentiation among catchments combined with high levels of inbreeding within populations. For chloroplast microsatellites, the first two DAPC axes explained 56.5% of the total variance (Fig. 6A). Individuals again formed three main groups, with stronger separation among catchments than observed for nuclear markers. Nevertheless, some individuals showed mixed ancestry, indicating limited but detectable seed-

mediated gene flow. Clusters were also supported by UPGMA analyses (Fig. 6B). AMOVA based on chloroplast microsatellites revealed strong population structure, with the majority of genetic variation occurring among catchments ($\Phi_{ST} = 0.78$, $p < 0.01$), consistent with restricted seed-mediated gene flow. In contrast to nuclear markers, within-population variation was comparatively low, highlighting the stronger spatial structuring of maternally inherited variation.

3.3.2 Pollen versus seed dispersal among catchments

Estimated migration rates indicated contrasting dispersal patterns for pollen and seed. Mean pollen migration among catchments was low (mean = 0.06; range = 0.01–0.21), whereas mean seed migration was substantially higher (mean = 0.30; range = 0.14–0.41). The pollen-to-seed migration ratio (mp/ms = 0.136) suggests that seed dispersal contributes more strongly than pollen dispersal to gene flow among catchments in *M. germanica*.

3.4 Migration patterns

3.4.1 Historical nuclear versus chloroplast migration

Historical relative nuclear migration rates among river catchments estimated from nuclear microsatellites inferred using MIGRATE-n were uniformly high (0.19–0.75) (Table S5–S6, Appendix 1). These estimates indicate pervasive historical nuclear gene flow, with no population approaching isolation. Directionality remained biologically meaningful; however, relative differences among migration pathways were more informative than absolute M values (Appendix 1; Fig. 7A). Bayesian estimates of mutation-scaled migration rates based on chloroplast markers revealed generally low but highly directional historical gene flow. Only a subset of migration

pathways showed strong posterior support for non-zero migration, while many credible intervals overlapped zero (Appendix 2, Fig. 7B, Table S7-S8). A comparison between nuclear and chloroplast markers further revealed contrasting modes of dispersal. Nuclear markers showed higher and more symmetrical migration rates, consistent with extensive pollen-mediated gene flow across catchments. In contrast, chloroplast DNA exhibited lower and more directional migration, reflecting the more restricted nature of seed dispersal. This distinction is expected because biparentally inherited nuclear markers are dispersed via both pollen and seed, whereas maternally inherited markers such as chloroplast DNA are primarily transmitted through seeds (Petit et al. 2005; Zhang & Hewitt 2003). Empirical studies consistently show that pollen-mediated dispersal often exceeds seed dispersal by orders of magnitude, enabling gene flow over larger spatial scales (Petit et al. 2005; Zhang & Hewitt 2003). Population-specific patterns reinforced this interpretation. For example, Po received substantial nuclear gene flow but comparatively little chloroplast input, suggesting limited seed immigration. Isar functioned as both a donor and recipient for nuclear markers but was primarily a recipient for chloroplast variation, indicating asymmetric seed dispersal. In contrast, Tagliamento showed high migration rates for both marker types, implying that it is not only a sink for pollen but also a key recipient (and possibly source) of seeds. Together, these findings demonstrate that pollen dispersal drives widespread and multidirectional connectivity, whereas seed dispersal is more spatially constrained, generating stronger population structure in maternally inherited genomes (Appendix 1, Appendix 2, Figure 7 A-B).

3.4.2 Contemporary seed migration

Contemporary migration estimated with BA3 revealed low seed-mediated migration among catchments (mean $m \pm SD = 0.025 \pm 0.006$) and genetic exchange occurring almost exclusively within catchments (mean $m \pm SD = 0.75 \pm 0.02$). Nonetheless, limited gene flow among clusters was detected (Fig. 7C, Appendix S3, Table S9). Some catchments contributed disproportionately to the gene pool of *M. germanica*, particularly Tagliamento, Rhine, Lech, Inn, and Isar. Inbreeding coefficients were high across all 12 catchments (mean $\pm SD = 0.72 \pm 0.035$; Appendix S3).

4 Discussion

Using nuclear and chloroplast microsatellite markers, we investigated genetic diversity, population structure, and gene flow in *M. germanica* across 67 populations spanning 12 major catchments in Central Europe. Across marker types and analytical approaches, our results consistently indicate low genetic diversity, high inbreeding, strong population differentiation, and restricted contemporary connectivity among catchments. From a conservation genetics perspective, these patterns are concerning because reduced genetic diversity and elevated inbreeding may limit the evolutionary potential of populations and reduce their ability to respond to future environmental change (Reed & Frankham 2003; Hedrick 2005). Migration analyses further reveal pronounced spatial asymmetries and clear contrasts between pollen- and seed-mediated dispersal, demonstrating how dispersal vectors operating over different temporal scales jointly shape the genetic structure of this threatened riparian species. The strong genetic structuring observed across river systems suggests that contemporary river catchments represent biologically meaningful evolutionary units for conservation and management.

Genetic diversity, inbreeding, and population structure in a conservation context

475
476 Low genetic diversity and high inbreeding coefficients across populations are
477 consistent with expectations for riparian pioneer plants combining self-pollination with
478 frequent demographic turnover (Reed & Frankham 2003; Werth & Scheidegger 2014;
479 Fink et al. 2022). Recurrent founder events during colonization, coupled with
480 population bottlenecks driven by river dynamics, likely reduce effective population
481 size and elevate inbreeding, even in the absence of strong geographic isolation.
482 Such reductions in effective population size are of particular conservation concern
483 because they increase the influence of genetic drift and may accelerate the loss of
484 adaptive genetic variation over time (Reed & Frankham 2003; Hedrick 2005).
485 High genetic differentiation among populations, reflected in elevated pairwise F_{ST}
486 values for both nuclear and chloroplast markers, reinforces this interpretation.
487 Although isolation by distance was detected at the regional scale, substantial
488 differentiation also occurred within catchments, indicating that local riverscape
489 features, including channel morphology and anthropogenic barriers, limit dispersal
490 along river corridors (Werth et al. 2014; Fink et al. 2022). This finding suggests that
491 habitat fragmentation and altered river dynamics may have reduced effective
492 connectivity among populations within catchments. Consequently, genetic diversity is
493 increasingly partitioned among populations rather than shared across the landscape,
494 increasing the importance of conserving multiple populations and catchments to
495 preserve the species' overall genetic diversity.
496 The observed genetic structure provides a direct framework for interpreting migration
497 patterns. High differentiation, low diversity, and elevated inbreeding collectively
498 indicate limited effective gene flow among populations. This is consistent with low
499 contemporary migration rates inferred from BA3 and the strong structuring observed
500 among catchments. The substantial proportion of genetic variation partitioned among

catchments further suggests that these river systems may function as management units from a conservation genetics perspective, each contributing unique components of the species' genetic diversity (Petit et al. 2005; Coates et al. 2018). Preserving connectivity within and among these units may therefore be critical for maintaining long-term evolutionary processes while avoiding further erosion of genetic diversity.

Contrasting nuclear and chloroplast structure: implications for connectivity and conservation

Differences between nuclear and chloroplast genetic structure provide important insights into the mechanisms maintaining connectivity in fragmented populations of *M. germanica*. Chloroplast microsatellites showed stronger population structure and lower admixture than nuclear markers, consistent with the smaller effective population size and uniparental inheritance of organellar genomes (Petit et al. 2005; Zhang & Hewitt 2003). This pattern indicates that seed dispersal is considerably more spatially restricted than pollen dispersal and suggests that effective demographic connectivity among populations is limited. From a conservation perspective, restricted seed dispersal may constrain natural recolonization of suitable habitats and reduce the capacity of populations to recover following local extinctions. At the catchment scale, nuclear data (reflecting pollen and seed dispersal) showed clearer isolation by distance than chloroplast data, whereas chloroplast structure deviated from simple geographic expectations. This suggests that seed-mediated dispersal is influenced by hydrological connectivity, historical contingencies, and stochastic colonization events rather than geographic distance alone (Nilsson et al. 2010; Werth et al. 2014; Auffret et al. 2015). Similar decoupling between pollen- and seed-mediated dispersal has been reported in other riparian and woody plant species (Ennos 1994; Petit et al. 2005; Ngeve et al. 2017). The strong differentiation of chloroplast genetic markers observed among catchments indicates that individual

river systems retain unique components of the species' evolutionary history and therefore represent important reservoirs of genetic diversity. Migration analyses reinforce this contrast. Nuclear gene flow was generally higher and more symmetrical, indicating widespread pollen-seed mediated connectivity. In contrast, chloroplast gene flow was limited and directional, with clear source–sink patterns. For example, Po received substantial nuclear gene flow but little chloroplast input, indicating limited seed immigration. Isar functioned as both donor and recipient for nuclear markers but primarily as a chloroplast sink, suggesting restricted seed export. Tagliamento exhibited high migration rates for both marker types, identifying it as a key node for both pollen- and seed-mediated connectivity. These results suggest that while pollen dispersal may partially counteract genetic isolation, seed-mediated demographic connectivity remains limited, increasing the importance of maintaining habitat continuity and dispersal corridors within catchments.

Historical versus contemporary gene flow

Migration analyses highlight a strong temporal contrast in gene flow. Historical nuclear migration rates inferred with MIGRATE-n were uniformly high, indicating extensive pollen-mediated connectivity across catchments over evolutionary timescales (Beerli & Felsenstein 2001; Ennos 1994). No population showed evidence of long-term isolation, and several catchments consistently acted as major sources or sinks of gene flow. The observed asymmetry, including the central role of the Rhine and the sink-like behaviour of the Tagliamento, suggests that historical connectivity was widespread despite geographic structuring. In contrast, chloroplast migration estimates revealed fewer and more directional seed dispersal pathways, with strong support for only a limited number of connections (Fig 7.B). This indicates that seed-mediated gene flow has historically been rare but is

evolutionarily important, likely occurring through major hydrological linkages and episodic long-distance dispersal events (Hewitt 2000; Hewitt 2004; Nilsson et al. 2010). Contemporary migration analyses further show that seed-mediated gene flow is now largely confined within catchments, with only limited exchange among them (Wilson & Rannala 2003; Werth & Scheidegger 2014).

The contrast between historically extensive connectivity and currently restricted dispersal suggests that contemporary populations may be experiencing increasing genetic isolation. Such reductions in connectivity can accelerate genetic drift, promote further inbreeding, and reduce adaptive potential, particularly in species already characterized by low genetic diversity (Reed & Frankham 2003; Hedrick 2005). Maintaining or restoring connectivity among populations may therefore be critical for preserving long-term evolutionary processes in *M. germanica*.

Alpine glaciation and postglacial recolonization: conserving historical genetic legacies

The contrasting spatial signatures of nuclear and chloroplast gene flow are consistent with the legacy of Alpine glaciation and postglacial recolonization. During the Pleistocene glacial maxima, *M. germanica* was likely confined to refugia in low-elevation river valleys (Taberlet et al. 1998; Hewitt 2000; Schönswetter et al. 2005). Postglacial expansion likely occurred along river corridors, generating directional patterns in chloroplast variation that remain detectable today (Hewitt 2004; Nilsson et al. 2010).

The strong chloroplast structure and limited seed-mediated connectivity suggest recolonization through a relatively small number of dispersal routes rather than widespread expansion. In contrast, extensive nuclear connectivity likely reflects prolonged pollen-mediated gene flow following recolonization, which homogenized nuclear variation while preserving historical chloroplast signatures (Ennos 1994; Petit

et al. 2005). The asymmetric gene flow observed among catchments, including the accumulation of diversity in systems such as the Tagliamento and the central role of the Rhine, is consistent with long-term dispersal along major river corridors facilitating secondary contact among lineages (Tockner & Stanford 2002; Burkhardt-Holm et al. 2002; Weiss et al. 2018).

From a conservation perspective, these patterns suggest that contemporary populations preserve both historical and contemporary components of genetic diversity. Catchments exhibiting unique chloroplast lineages or acting as repositories of genetic variation (e.g Isar and Tagliamento) may therefore represent particularly valuable conservation targets because they capture evolutionary processes operating over both ecological and geological timescales.

These patterns support a two-phase postglacial history: an initial phase dominated by rare, directional seed dispersal, followed by prolonged pollen-mediated gene flow maintaining nuclear connectivity.

Conservation implications

Our results indicate that river catchments represent biologically meaningful management units for *M. germanica*, particularly with respect to seed-mediated dispersal and local demographic processes. Strong population differentiation limited contemporary seed-mediated gene flow, and elevated inbreeding suggest that populations within catchments are becoming increasingly isolated. Consequently, the loss of individual populations may result in the irreversible loss of unique genetic variation and historical lineages that are not readily replenished through natural recolonization (Petit et al. 2005; Reed & Frankham 2003).

The restricted connectivity observed among catchments further suggests that demographic rescue through natural dispersal is likely to be limited. Therefore,

605 conservation efforts should prioritize the maintenance and restoration of within-
606 catchment connectivity through the preservation of natural river dynamics, active
607 gravel-bar habitats, and hydrological processes that facilitate seed dispersal and
608 population establishment (Fausch et al. 2002; Bunn & Arthington 2002; Werth et al.
609 2014). Because effective seed dispersal appears to be substantially more restricted
610 than pollen dispersal, habitat restoration aimed at promoting recruitment and
611 establishment may be particularly important for maintaining demographic
612 connectivity.

613 At broader spatial scales, the persistence of pollen-mediated connectivity highlights
614 the importance of maintaining landscape permeability and functional dispersal
615 corridors. Large catchments such as the Rhine appear to function as regional genetic
616 hubs that facilitate genetic exchange across the landscape, whereas systems such
617 as the Tagliamento act as important reservoirs of genetic diversity through the
618 accumulation of migrants from multiple sources. These catchments may therefore
619 represent high-priority conservation areas because they contribute disproportionately
620 to the maintenance of regional genetic diversity and evolutionary processes.

621 The strong differentiation observed among catchments also suggests that they
622 should be considered candidate management units within a conservation biology
623 framework. Conservation planning should therefore aim to preserve genetic diversity
624 both within and among catchments rather than focusing exclusively on individual
625 populations. Such an approach would maximize the retention of evolutionary
626 potential and enhance the long-term capacity of *M. germanica* to respond to future
627 environmental change. Given the status of *M. germanica* as indicator and keystone
628 species in their specialized habitat and vegetation types (European Environment

Agency 2013; Evans & Roekaerts 2019), the long-term conservation of *M. germanica* will help support alpine riparian habitats.

Conclusions

Myricaria germanica populations across Central Europe are characterized by low genetic diversity, high inbreeding, and strong spatial genetic structure. These patterns likely reflect the combined effects of selfing, restricted seed dispersal, historical demographic processes, and the fragmented nature of contemporary riverine habitats. The pronounced genetic differentiation among populations and catchments indicates that substantial components of the species' genetic diversity are partitioned across the landscape, emphasizing the importance of conserving multiple populations throughout the range of this species.

By combining data from nuclear and chloroplast microsatellites, we demonstrate that pollen- and seed-mediated dispersal contribute differently to connectivity. Extensive pollen-mediated gene flow has historically maintained genetic exchange among catchments, whereas seed-mediated dispersal remains highly restricted and spatially structured. This asymmetry has generated distinct source–sink dynamics and contributed to the strong chloroplast structure observed throughout the species' range.

The contrasting signatures of historical and contemporary connectivity suggest that present-day populations retain genetic legacies of postglacial recolonization while simultaneously experiencing increasing demographic and genetic isolation.

Maintaining connectivity within river systems, preserving genetically important catchments, and protecting the natural processes that generate suitable riparian habitats will therefore be essential for safeguarding both contemporary genetic diversity and the long-term evolutionary potential of *M. germanica*. Overall, our

findings highlight the value of integrating historical and contemporary perspectives on gene flow to inform conservation strategies for threatened riparian species as well as their unique habitats.

Acknowledgments

Logistics support was received from the Genetic Diversity Centre (GDC) of ETH Zürich, from the WSL, from the University of Iceland and from the LMU Munich. We thank A. Minder and T. Torrossi (GDC) for running fragment analyses on an automatic sequencer. The data generation was kindly funded by the Swiss Federal Office of the Environment, BAFU, via the research program Hydraulic Engineering and Ecology. Barbara Krummenacher collected many of the samples included in this study. We thank S. Angelone, T. Karpati and C. Spinelli for helping with the fieldwork. S. Cheenacharoen and Y. Kophimai helped with extracting DNA. TCP's salary was funded by a grant from the German Research Foundation DFG to SW (grant number WE 6443/1-1).

Conflict of interest

None declared.

Author contributions

Conceived and designed the experiments: SW, CS. Performed the experiments: SW. Generated all data: SW. Analyzed the data: SW, TCP. Made the figures: TCP. Improved the figures: KW. Wrote the paper: TCP. Edited the manuscript: CS, KW, SW, TCP. Aquired funding: CS, SW.

Data availability statement

679 The microsatellite data of the nuclear loci and the chloroplast loci, the population and
680 individual information of the samples and the R script containing all analyses have
681 been deposited under the following link:
682 <https://figshare.com/s/13083619cea77f51ab22>

REFERENCES

- Aradottir, A. L., Svavarsdottir, K., & Bau, A. (2007). Clonal variability of native willows (*Salix phylicifolia* and *Salix lanata*) in Iceland and implications for use in restoration. *Icelandic Agricultural Sciences* 20, 61–72.
- Asztalos, M., Glaw, F., Franzen, M., Kindler, C., & Fritz, U. (2021). Transalpine dispersal: Italian barred grass snakes in southernmost Bavaria – this far but no further! *Journal of Zoological Systematics and Evolutionary Research* 59, 1136–1148.
<https://doi.org/10.1111/jzs.12471>
- Auffret, A. G., Plue, J., & Cousins, S. A. O. (2015). The spatial and temporal components of functional connectivity in fragmented landscapes. *AMBIO* 44, 51–59.
<https://doi.org/10.1007/s13280-014-0588-6>
- Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience* 54, 413–427.
[https://doi.org/10.1641/0006-3568\(2004\)054\[0413:TNDHHC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2)
- Beerli, P., & Felsenstein, J. (2001). Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences USA* 98, 4563–4568.
<https://doi.org/10.1073/pnas.08106809>
- Beerli, P. (2016). MIGRATE-N: estimation of population sizes and gene flow using the coalescent. *Molecular Ecology Resources* 16, 120–123.
<https://doi.org/10.1111/1755-0998.12471>
- Birks, H. H., & Ammann, B. (2000). Two terrestrial records of rapid climatic change during the glacial–Holocene transition (14,000–9,000 calendar years BP) from Europe. *Proceedings of the National Academy of Sciences USA* 97, 1390–1394.
<https://doi.org/10.1073/pnas.97.4.1390>
- Blattner, L., Lucek, K., Beck, N., Berner, D., & von Fumetti, S. (2022). Intra-Alpine islands: population genomic inference reveals high degrees of isolation between freshwater spring habitats. *Diversity and Distributions* 28, 291–305.
<https://doi.org/10.1111/ddi.13461>
- Broquet, T., Angelone, S., Jaquiere, J., Joly, P., Léna, J.-P., Lengagne, T., Plénet, S., Luquet, E., & Perrin, N. (2010). Genetic bottlenecks driven by population disconnection. *Conservation Biology* 24, 1596–1605.
<https://doi.org/10.1111/j.1523-1739.2010.01556.x>
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30, 492–507.
<https://doi.org/10.1007/s00267-002-2737-0>
- Burkhardt-Holm, P., Peter, A., & Segner, H. (2002). The Rhine: ecological and evolutionary significance of a large European river. *Aquatic Sciences* 64, 127–143.
<https://doi.org/10.1007/BF02272234>
- Dansgaard, W., Johnsen, S. J., Clausen, H. B., *et al.* (1993). Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–

220.
<https://doi.org/10.1038/364218a0>
- Davis, C. D., Epps, C. W., Flitcroft, R. L., & Banks, M. A. (2018). Refining and defining riverscape genetics: how rivers influence population genetic structure. *Wiley Interdisciplinary Reviews: Water* 5, e1269.
<https://doi.org/10.1002/wat2.1269>
- Djedid, I. K., Terzaghi, M., Brundu, G., *et al.* (2022). Genetic diversity and differentiation of eleven *Medicago* species revealed by nuclear and chloroplast microsatellite markers. *Genes* 13, 97.
<https://doi.org/10.3390/genes13010097>
- Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* 4, 359–361.
<https://doi.org/10.1007/s12686-011-9548-7>
- Egelund, B., Pertoldi, C., & Barfod, A. S. (2012). Isolation and reduced gene flow among Faroese populations of *Salix phylicifolia*. *New Journal of Botany* 2, 9–15.
<https://doi.org/10.1179/2042349712Y.0000000003>
- Ennos, R. A. (1994). Estimating the relative rates of pollen and seed migration among plant populations. *Heredity* 72, 250–259.
<https://doi.org/10.1038/hdy.1994.33>
- European Environment Agency. (2013). NATURA 2000: Interpretation Manual of European Union Habitats version EUR28. Directorate-General for Environment, European Commission, Brussels, Belgium.
- Excoffier, L., Laval, G., & Schneider, S. (2005). Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics* 1, 47–50.
<https://doi.org/10.1177/117693430500100003>
- Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* 14, 2611–2620.
<https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Evans, D., & Roekaerts, M. (2019). Interpretation manual of the habitats listed in Resolution No. 4 (1996) listing endangered natural habitats requiring specific conservation measures. Tech. rep. T-PVS/PA (2019) 18. Fourth draft version. Council of Europe, Standing Committee to the Bern Convention.
- Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52, 483–498.
[https://doi.org/10.1641/0006-3568\(2002\)052\[0483:LTRBTG\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2)
- Fink S, T. Lanz, R. Stecher, & Christoph Scheidegger. (2017). Colonization potential of an endangered riparian shrub species. *Biodiversity and Conservation*, 26(9), 2099–2114.
<https://doi.org/10.1007/s10531-017-1347-3>
- Fink, S. A. Hoppler-Wiedmer, Z. Zengerer, G. Egger, M. Schletterer & C. Scheidegger. (2022). Gene flow in a pioneer plant metapopulation (*Myricaria germanica*) at the catchment scale in a fragmented alpine river system. *Scientific Reports* 12, 8570.
<https://doi.org/10.1038/s41598-022-12172-x>

- Goldstein, D. B., and D. D. Pollock. 1997. Launching microsatellites: A review of mutation processes and methods of phylogenetic inference. *Journal of Heredity* 88:335-342.
- Gostner, W., M. Paternolli, A. Schleiss, C. Scheidegger, and S. Werth. 2017. Gravel bar inundation frequency: an important parameter for understanding riparian corridor dynamics. *Aquatic Sciences* 79:825-839.
- Grivet, D., Deguilloux, M. F., Petit, R. J., & Sork, V. L. (2006). Contrasting patterns of historical colonization in white oaks in California and Europe. *Molecular Ecology* 15, 4085–4093.
<https://doi.org/10.1111/j.1365-294X.2006.03083.x>
- Hedrick, P. W. (2005). A standardized genetic differentiation measure. *Evolution* 59, 1633–1638.
<https://doi.org/10.1111/j.0014-3820.2005.tb01814.x>
- Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature* 405, 907–913.
<https://doi.org/10.1038/35016000>
- Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B* 359, 183–195.
<https://doi.org/10.1098/rstb.2003.1388>
- Honnay, O., H. Jacquemyn, K. Nackaerts, P. Breyne, and K. Van Looy. 2010. Patterns of population genetic diversity in riparian and aquatic plant species along rivers. *Journal of Biogeography* 37:1730-1739.
- Liu, Y., Y. Wang, and H. Huang. 2006. High interpopulation genetic differentiation and unidirectional linear migration patterns in *Myricaria laxiflora* (Tamaricaceae), an endemic riparian plant in the Three Gorges valley of the Yangtze River. *American Journal of Botany* 93:206-215
- Love, H. M., C. A. Maggs, T. E. Murray, and J. Provan. 2013. Genetic evidence for predominantly hydrochoric gene flow in the invasive riparian plant *Impatiens glandulifera* (Himalayan balsam). *Annals of Botany* 112:1743-1750.
- Kudrnovsky, H., & Stöhr, O. (2013). *Myricaria germanica* (L.) Desv. historisch und aktuell in Österreich: ein dramatischer Rückgang einer Indikatorart von europäischem Interesse. *Stapfia* 99: 13–34.
- Nilsson, C., Brown, R. L., Jansson, R., & Merritt, D. M. (2010). The role of river corridors in plant dispersal and diversity. *Biological Reviews* 85, 837–858.
<https://doi.org/10.1111/j.1469-185X.2010.00153.x>
- Parisod, C. (2022). Plant speciation in the face of recurrent climate changes in the Alps. *Alpine Botany* 132, 21–28.
<https://doi.org/10.1007/s00035-021-00259-6>
- Petit, R. J., Aguinagalde, I., de Beaulieu, J.-L., et al. (2003). Glacial refugia: hotspots but not melting pots of genetic diversity. *Science* 300, 1563–1565.
<https://doi.org/10.1126/science.1083264>
- Petit, R. J., Duminil, J., Fineschi, S., et al. (2005a). Comparative organization of chloroplast, mitochondrial and nuclear diversity in plant populations. *Molecular Ecology* 14, 689–701.
<https://doi.org/10.1111/j.1365-294X.2004.02410.x>

- Petit, R. J., Hampe, A., & Cheddadi, R. (2005b). Climate changes and tree phylogeography in the Mediterranean. *Taxon* 54, 877–885.
<https://doi.org/10.2307/25065568>
- Sun, K., & Werth, S. (2024). Journey to the west: Migration patterns of the riparian montane genus *Myricaria*. *Flora* 321, 152639.
<https://doi.org/10.1016/j.flora.2024.152639>
- Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environmental Conservation* 29, 308–330.
<https://doi.org/10.1017/S037689290200021X>
- Webb, D. A. (1968). *Myricaria* Desv. In T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb [eds.], *Flora Europaea*, vol. 2. Cambridge University Press, Cambridge, United Kingdom.
- Weiss, S., Macher, J.-N., Seifert, K., & Leese, F. (2018). Glacial refugia, postglacial expansion and rivers as genetic corridors in European freshwater organisms. *Freshwater Biology* 63, 1074–1088.
<https://doi.org/10.1111/fwb.13106>
- Weitkämper, K., Rückschloß, K., Sitzia, T., Michielon, B., Werth, S., & Weitkämper, F. (2026). Pearl's causality for integrating ecological datasets: A case study on *Myricaria germanica* in northern Italy. *Applications in Plant Sciences* 14: e70056.
<https://doi.org/10.1002/aps3.70056>
- Werth, S., & Scheidegger, C. (2011). Isolation and characterization of nuclear and chloroplast microsatellite loci in *Myricaria germanica*. *Conservation Genetics Resources* 3, 445–448.
<https://doi.org/10.1007/s12686-010-9376-1>
- Werth, S., Schödl, M., & Scheidegger, C. (2014). Dams and canyons disrupt gene flow among populations of a threatened riparian plant. *Freshwater Biology* 59, 2502–2515.
<https://doi.org/10.1111/fwb.12449>
- Werth, S., & Scheidegger, C. (2014). Gene flow within and between catchments in *Myricaria germanica*. *PLoS ONE* 9, e99400.
<https://doi.org/10.1371/journal.pone.0099400>
- Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38, 1358–1370.
<https://doi.org/10.2307/2408641>
- Wilson, G. A., & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163, 1177–1191.
<https://doi.org/10.1093/genetics/163.3.1177>
- Zhang, D.-X., & Hewitt, G. M. (2003). Nuclear DNA analyses in genetic studies of populations: practice, problems and prospects. *Molecular Ecology* 12, 563–584.
<https://doi.org/10.1046/j.1365-294X.2003.01773.x>

882 **Table1.** Location information for 67 populations of *Myricaria germanica*. Shown are the number of samples per population (N),
883 geographic coordinates (map datum WGS84), elevation (m), country, catchment and major catchment the populations belong to.
884

Population	N	Latitude	Longitude	Elevation	Country	Catchment	Major catchment
ADD1	22	46.23605	10.22000	610	Italy	Po	Po
ADD2	18	46.33141	10.33000	900	Italy	Po	Po
ADD3	9	46.32695	10.33376	880	Italy	Po	Po
AMM1	15	47.773729	11.00389	620	Germany	Isar	Danube
BED1	40	46.50508	8.52455	1335	Switzerland	Po	Po
CZE1	32	49.638794	18.44105	380	Czech Republic	Oder	Danube
HAL1	40	47.649674	10.79631	780	Germany	Lech	Danube
INN1	44	46.480341	9.919276	1840	Switzerland	Inn	Danube
INN2	44	46.552636	9.871962	1750	Switzerland	Inn	Danube
INN3	44	46.478693	9.892024	1810	Switzerland	Inn	Danube
INN4	40	46.446552	9.94274	1915	Switzerland	Inn	Danube
INN5	40	46.601308	9.970937	1840	Switzerland	Inn	Danube
INN6	40	46.858684	10.43031	1060	Switzerland	Inn	Danube
INN7	9	46.396107	9.751708	2000	Switzerland	Inn	Danube
INN8	40	46.853896	10.42408	1115	Switzerland	Inn	Danube
INN9	40	46.610131	10.02361	1720	Switzerland	Inn	Danube
IS10	40	47.530389	11.32675	880	Germany	Isar	Danube
ISA2	39	47.417991	11.25660	930	Germany	Isar	Danube
ISA3	3	47.422776	11.25932	1000	Germany	Isar	Danube
ISA4	40	47.478861	11.28016	350	Germany	Isar	Danube
ISA5	40	47.552252	11.40353	800	Germany	Isar	Danube
ISA6	40	47.597204	11.55688	740	Germany	Isar	Danube
ISA7	5	47.480387	11.27961	930	Germany	Isar	Danube
ISA8	40	47.55205	11.41287	800	Germany	Isar	Danube
ISA9	40	47.471806	11.28091	350	Germany	Isar	Danube
ISE1	40	46.91569	12.60856	770	Austria	Drau	Danube
KAN1	39	46.460681	7.674966	1380	Switzerland	Aare	Rhine

887 **Table 1. Continued**

888

Population	N	Latitude	Longitude	Elevation	Country	Catchment	Major catchment
LEC1	40	47.43003	10.60328	950	Austria	Lech	Danube
LEC2	39	47.42203	10.57707	920	Austria	Lech	Danube
LEC3	40	47.43238	10.62825	887	Austria	Lech	Danube
LEC4	40	47.3286	10.52215	1028	Austria	Lech	Danube
LEC5	7	47.5546	10.67406	800	Austria	Lech	Danube
LEC6	32	47.40072	10.57254	930	Austria	Lech	Danube
LEC7	40	47.4129	10.57775	910	Austria	Lech	Danube
MAG1	40	46.265588	8.682544	340	Switzerland	Po	Po
MAG2	40	46.294008	8.632446	374	Switzerland	Po	Po
MÄI1	43	46.39794	9.684693	1580	Switzerland	Po	Po
MÄI2	53	46.34994	9.612635	1060	Switzerland	Po	Po
MÄI3	15	46.33041	9.50454	640	Switzerland	Po	Po
MOE1	40	46.247523	9.15604	302	Switzerland	Po	Po
MRH1	40	46.6743	8.854504	1250	Switzerland	Rhine	Rhine
RHE1	41	46.939694	9.546762	540	Switzerland	Rhine	Rhine
RHE2	47	46.786434	9.410571	610	Switzerland	Rhine	Rhine
RHE3	47	47.073971	9.491499	470	Switzerland	Rhine	Rhine
RHE4	43	46.960477	9.54792	570	Switzerland	Rhine	Rhine
RHE5	19	47.27791	9.54192	410	Switzerland	Rhine	Rhine
RHE6	17	47.0193	9.50798	500	Switzerland	Rhine	Rhine
RHO1	44	46.302413	7.575609	540	Switzerland	Rhône	Rhône
RHO2	43	46.126273	7.630048	1674	Switzerland	Rhône	Rhône
RHO3	40	46.306314	7.585912	560	Switzerland	Rhône	Rhône
RIS1	8	47.534083	11.44013	81	Germany	Isar	Danube
ROM1	40	46.65127	10.48261	1100	Italy	Adige	Adige
SEN1	41	46.734403	7.296919	829.5	Switzerland	Aare	Rhine
TA10	39	46.2123	13.0179	155	Italy	Tagliamento	Tagliamento
TAG1	46	46.38588	12.67208	690	Italy	Tagliamento	Tagliamento
TAG2	19	46.41395	13.00841	330	Italy	Tagliamento	Tagliamento

889

890

891 **Table 1.** Continued.

892

Population	N	Latitude	Longitude	Elevation	Country	Catchment	Major catchment
TAG3	40	46.41818	13.0095	340	Italy	Tagliamento	Tagliamento
TAG4	40	46.36391	13.11175	230	Italy	Tagliamento	Tagliamento
TAG5	2	46.30754	13.11676	230	Italy	Tagliamento	Tagliamento
TAG6	42	46.39952	13.20573	308	Italy	Tagliamento	Tagliamento
TAG7	43	46.20287	12.97113	140	Italy	Tagliamento	Tagliamento
TAG8	42	46.20678	12.99471	140	Italy	Tagliamento	Tagliamento
TAG9	44	46.21103	13.00997	150	Italy	Tagliamento	Tagliamento
UKR1	30	48.894583	22.77319	510	Ukraine	Lyuta	Danube
VRH1	41	46.785215	9.240862	900	Switzerland	Rhine	Rhine
VRH2	40	46.772721	9.175004	710	Switzerland	Rhine	Rhine
VRH4	41	46.727076	8.957355	900	Switzerland	Rhine	Rhine

893

894

895

896

897

898

899

900

901

902

903

904

905

906

907

908

Table 2. Population statistics for 67 geographically distinct populations of *M. germanica* based on twenty nuclear microsatellites. Shown are MLG, the number of multilocus genotypes; H, the Shannon-Wiener Diversity index; Hexp, expected heterozygosity; F_{IS} , Wright's inbreeding coefficient; and F_{ST} , fixation index of subpopulation to total.

Population	N	MLG	H	Hexp	Hobs	F_{IS}	F_{ST}
ADD1	22	4	0,548	0,511	0,989	0.60	0,881
ADD2	18	18	2,890	0,507	0,767	0.62	0,702
ADD3	9	8	2,043	0,501	0,789	0.59	0,720
AMM1	12	11	2,369	0,292	0,479	0.10	0,819
BED1	35	24	3,033	0,364	0,670	0.34	0,846
CZE1	32	4	0,414	0,208	0,400	0.58	0,906
HAL1	40	39	3,654	0,407	0,581	0.18	0,700
INN1	39	26	3,117	0,229	0,412	0.66	0,809
INN2	40	31	3,329	0,228	0,400	0.77	0,804
INN3	40	17	2,553	0,210	0,389	0.93	0,816
INN4	40	29	3,175	0,226	0,389	0.67	0,826
INN5	40	29	3,210	0,242	0,413	0.72	0,814
INN6	39	39	3,664	0,459	0,618	0.15	0,642
INN7	9	5	1,427	0,254	0,461	0.80	0,837
INN8	34	34	3,526	0,451	0,632	0.40	0,629
INN9	38	15	2,126	0,254	0,459	0.83	0,821
IS10	40	40	3,689	0,458	0,625	0.30	0,612
ISA2	3	3	1,099	0,444	0,683	0.18	0,665
ISA3	17	16	2,752	0,381	0,606	0.51	0,691
ISA4	37	37	3,611	0,468	0,647	0.26	0,620
ISA5	40	40	3,689	0,465	0,674	0.21	0,616
ISA6	38	38	3,638	0,453	0,601	0.11	0,606
ISA7	5	5	1,609	0,454	0,680	0.14	0,625
ISA8	32	32	3,466	0,450	0,617	0.07	0,619
ISA9	38	38	3,638	0,478	0,657	0.17	0,617
ISE1	39	37	3,579	0,406	0,687	0.17	0,745
KAN1	37	37	3,611	0,379	0,609	0.35	0,805
LEC1	40	40	3,689	0,479	0,638	0.21	0,597
LEC2	39	39	3,664	0,476	0,699	0.40	0,614
LEC3	35	35	3,555	0,457	0,621	0.13	0,606
LEC4	40	40	3,689	0,454	0,621	0.23	0,620
LEC5	7	6	1,748	0,404	0,571	0.23	0,636
LEC6	29	28	3,319	0,444	0,603	0.24	0,608
LEC7	35	34	3,516	0,431	0,573	0.32	0,617
MAG1	38	36	3,551	0,466	0,657	0.31	0,723
MAG2	39	39	3,664	0,466	0,646	0.24	0,721
MÄI1	43	10	1,564	0,242	0,451	0.36	0,845

920 **Table 2.** Continued.

921

Population	N	MLG	H	Hexp	Hobs	F_{IS}	F_{ST}
MÄI2	53	31	3,100	0,330	0,608	0.37	0,806
MÄI3	15	11	2,246	0,281	0,477	0.85	0,788
MOE1	36	33	3,468	0,452	0,676	0.60	0,797
MRH1	40	38	3,606	0,416	0,634	0.82	0,743
RHE1	33	33	3,497	0,398	0,559	0.18	0,668
RHE2	40	40	3,689	0,408	0,600	0.18	0,685
RHE3	44	43	3,753	0,417	0,607	0.27	0,663
RHE4	40	38	3,620	0,382	0,565	0.32	0,677
RHE5	18	3	0,426	0,277	0,517	0.27	0,844
RHE6	17	17	2,833	0,420	0,638	0.35	0,659
RHO1	44	44	3,784	0,443	0,633	0.40	0,653
RHO2	38	7	1,048	0,282	0,541	0.41	0,862
RHO3	36	33	3,429	0,459	0,618	0.45	0,679
RIS1	8	8	2,079	0,426	0,650	0.36	0,629
ROM1	40	39	3,654	0,428	0,691	0.04	0,758
SEN1	38	1	0,000	0,325	0,650	0.26	0,903
TA10	39	32	3,379	0,458	0,799	0.30	0,697
TAG1	46	4	0,548	0,433	0,851	0.55	0,814
TAG2	19	8	1,858	0,431	0,826	0.90	0,775
TAG3	39	21	2,725	0,437	0,806	0.79	0,717
TAG4	38	24	2,947	0,446	0,825	0.71	0,758
TAG5	2	2	0,693	0,394	0,775	0.41	0,763
TAG6	40	13	2,062	0,389	0,743	0.85	0,782
TAG7	42	28	3,127	0,450	0,814	0.69	0,718
TAG8	38	38	3,638	0,474	0,817	0.76	0,698
TAG9	42	38	3,593	0,452	0,804	0.53	0,708
UKR1	30	9	1,754	0,153	0,290	0.59	0,894
VRH1	41	37	3,578	0,349	0,579	0.68	0,730
VRH2	21	21	3,045	0,374	0,567	0.48	0,692
VRH4	41	41	3,714	0,457	0,623	0.34	0,687

922

923

924

925

926

927

928

929

930

931

932

933

934

935

936

Table 3. Genetic diversity and population differentiation for 67 populations of *M. germanica* based on haploid chloroplast microsatellites. Shown are sample size (N), Haplotype number, Shannon–Wiener diversity index (H), Φ ST (PhiST) which is the proportion of total genetic variance that is due to differences among populations.

Population	N	Haplotype	H	PhiST
ADD1	22	3	0,996	0,126
ADD2	18	3	0,849	0,340
ADD3	9	3	0,849	0,324
AMM1	12	1	0,000	0,150
BED1	39	5	0,996	0,334
CZE1	31	2	0,143	0,465
HAL1	40	2	0,500	0,320
INN1	39	5	0,998	0,331
INN2	40	5	0,715	0,390
INN3	39	3	0,859	0,328
INN4	40	4	0,349	0,427
INN5	40	3	1,090	0,277
INN6	39	3	0,320	0,138
INN7	9	3	0,937	0,284
INN8	34	1	0,000	0,173
INN9	38	3	1,018	0,289
IS10	40	4	0,349	0,137
IS12	39	5	0,869	0,071
ISA2	3	1	0,000	0,047
ISA3	17	1	0,000	0,160
ISA4	37	2	0,210	0,149
ISA5	40	5	0,464	0,128
ISA6	38	6	0,683	0,103
ISA7	5	2	0,500	0,028
ISA8	23	4	0,531	0,104
ISA9	40	1	0,000	0,176
ISE1	40	4	0,805	0,257
LEC1	40	4	1,116	0,024
LEC2	39	3	0,817	0,168
LEC3	35	5	1,088	0,046
LEC4	40	4	1,258	0,021
LEC5	7	3	0,796	0,019
LEC6	32	6	1,626	0,165
LEC7	40	6	1,467	0,140
MÄI1	43	4	1,070	0,301
MÄI2	53	3	0,187	0,161
MÄI3	15	7	1,767	0,233
MOE1	36	1	0,000	0,174

947 **Table 3.** Continued.
 948

Population	N	Haplotype	H	PhiST
RHE1	33	5	0,537	0,116
RHE2	40	2	0,117	0,163
RHE3	44	3	0,356	0,134
RHE4	40	3	0,381	0,129
RHE5	18	2	0,215	0,135
RHE6	17	2	0,224	0,132
RHO1	44	4	0,874	0,116
RHO2	38	3	0,243	0,149
RHO3	36	1	0,000	0,174
RHO4	1	1	0,000	-0,398
RIS1	8	3	0,900	0,017
ROM1	40	5	0,835	0,081
SEN1	39	1	0,000	0,175
TA10	39	4	0,837	0,215
TAG1	46	2	0,105	0,392
TAG2	19	4	0,734	0,279
TAG3	39	3	0,653	0,212
TAG4	36	3	0,613	0,237
TAG5	2	2	0,693	-0,213
TAG6	40	2	0,117	0,388
TAG7	42	4	0,555	0,314
TAG8	38	3	0,553	0,267
TAG9	42	4	0,685	0,285
UKR1	29	3	0,299	0,443
VRH1	41	1	0,000	0,176
VRH2	21	1	0,000	0,164

949
 950
 951
 952
 953
 954
 955
 956
 957
 958
 959
 960
 961
 962
 963
 964
 965
 966
 967

Table 4. Indices of genetic diversity per catchment calculated with nuclear data (diploid). Num (number of alleles), Eff_num (effective number of alleles), Ho (observed heterozygosity), Hs (expected heterozygosity), and F_{IS} (inbreeding coefficient).

Population	Num	Eff_num	Ho	Hs	F_{IS}
pop_Po	4.550	2.816	0.121	0.589	0.794
pop_Isar	4.400	1.816	0.279	0.399	0.300
pop_Oder	1.450	1.028	0.011	0.026	0.582
pop_Lech	4.350	1.830	0.279	0.391	0.286
pop_INN	4.100	1.731	0.091	0.400	0.773
pop_Drau	2.200	1.450	0.129	0.202	0.359
pop_Aare	2.350	1.743	0.087	0.372	0.765
pop_Rhine	5.100	2.411	0.227	0.482	0.530
pop_Rhone	3.500	1.790	0.182	0.360	0.494
pop_Adige	2.400	1.490	0.177	0.241	0.262
pop_Tagliamento	2.900	1.353	0.051	0.190	0.729
pop_Danube	1.200	1.131	0.025	0.079	0.682

Table 5. Genetic diversity indices of catchments, based on haploid chloroplast microsatellites. Haplotypes; Ne = effective number of haplotypes; H = haplotype diversity (Nei 1987).

Catchment	Haplotypes	H
Po	8.0	0.91
Isar	6.6	0.86
Oder	5.0	0.90
Lech	9.5	0.88
Inn	6.8	0.84
Drau	5.5	0.81
Rhine	5.75	0.88
Rhone	6.5	0.81
Adige	7.0	0.82
Aare	5.0	0.80
Tagliamento	5.6	0.86
Danube	5.5	0.90

991
992
993
994
995
996
997
998
999
1000
1001
1002
1003
1004

FIGURE 1. Map showing the geographic distribution of the 67 sampled populations of *Myricaria germanica* across 12 river catchments in Central Europe based on 2212 individuals. Populations are color-coded according to catchment.

FIGURE 2 Population genetic structure of *Myricaria germanica* based on 20 nuclear microsatellite loci. (A) Bayesian clustering analysis inferred with STRUCTURE. Each vertical bar represents an individual, and colors indicate membership coefficients for the two genetic clusters ($K = 2$) identified using the ΔK method. Individuals are grouped by population for visual clarity. (B) Discriminant analysis of principal components (DAPC) showing individual genotypes colored by population. The first two discriminant axes explain 80% of the total discriminant variance.

FIGURE 3. Geographic distribution of nuclear genetic clusters in *Myricaria germanica* across the 12 river catchments. Pie charts represent the mean assignment proportions (Q values) of the two STRUCTURE clusters ($K = 2$) for each population. Catchments with a single sampled population are shown with enlarged pie charts for clarity.

FIGURE 4. Population genetic structure in *Myricaria germanica* inferred from nuclear microsatellites. (A) DAPC scatterplot of individuals colored by catchment. The first two discriminant axes explain 82% of the total discriminant variance. (B) Unrooted maximum-likelihood tree of catchments based on nuclear genetic distances; bootstrap support (5000 replicates) is shown.

FIGURE 5. Population genetic structure of *Myricaria germanica* based on six chloroplast microsatellite loci. (A) STRUCTURE clustering performed in haploid mode. Each vertical bar represents an individual, and colors indicate cluster membership coefficients for $K = 2$. Results are shown descriptively to illustrate chloroplast lineage structure. (B) DAPC scatterplot of individuals colored by population. The first two discriminant axes explain 90% of the total discriminant variance.

FIGURE 6. Population genetic structure of *Myricaria germanica* inferred from chloroplast microsatellites. (A) DAPC scatterplot of individuals colored by catchment. The first two discriminant axes explain 88% of the total discriminant variance. (B) Unrooted maximum-likelihood tree of catchments based on chloroplast genetic distances; bootstrap support (5000 replicates) is shown.

FIGURE 7. Historical and contemporary migration patterns by seed and pollen dispersal of *Myricaria germanica*. (A) Historical migration among catchments inferred using MIGRATE-N based on nuclear data. We excluded from the analysis three catchments that only contained data from one single population (Oder, Danube and Aare) as these had a different geographic extent of sampling than the remaining catchments. Relative migration rates are represented by the proportion of colored segments within each circle. (B) Historical migration among catchments inferred using MIGRATE-N based on chloroplast haplotype. We excluded from the analysis three catchments that only contained data from one single population (Oder, Danube and Aare) as these had a different geographic extent of sampling than the remaining catchments.

1054 Relative migration rates are represented by the proportion of colored segments
1055 within each circle. (C) Contemporary migration among catchments inferred using all
1056 12 catchments by BayesAss. Migration proportions are represented by coloured
1057 segments within each circle.
1058
1059