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Gene flow in a highly dynamic habitat and a single founder event: Proof from a plant population on a relocated river site

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ABSTRACT

River relocations due to realization of infrastructure projects or flood protection provide a high potential for ecological restorations and the creation of near-natural habitats. Colonization success of new riparian habitats in the dynamic riverine zone is rarely predictable, as the survival of sessile plants is highly dependent on flood events. Relocated rivers offer a unique opportunity to study restoration success, and using genetic information allows tracing to source populations and assessing connectivity. This study focuses on the colonization of a new, 3.4 km long river stretch in the Inn catchment (Switzerland), with an artificial, stable shoreline and a dynamic riverine zone with gravel bars. We assess the colonization success of *Myricaria germanica*, a flagship species for floodplain pioneer vegetation, 14 years after river relocation. The population with over 600 individuals of which 147 were used for genetic analysis based on 22 microsatellite markers in comparison to 11 potential source populations up- and downstream of the new site. Our results on demography and genetic composition together with information on flood events allow tracing the origin of the subpopulation along the stable shoreline to a single founder event but several founder individuals further upstream. The subpopulation in the dynamic zone is younger and more likely strongly dependent on gene flow from the stable shoreline subpopulation, but allows for rejuvenation at the site. Genetic patterns along the catchment indicate ongoing gene flow, suggesting potential for colonization success for further restorations in the catchment. Our data reveals that near-natural flood dynamics with repeated larger flood events is a key factor for successful colonization of dynamic riparian habitats.

1. Introduction

Natural river dynamics were altered for e.g. flood protection measures, gravel excavation and for the gain of hydropower for centuries (Lytle and Poff, 2004). Beside modifications along rivers (e.g. building of dams, weirs or embankments), the relocation of whole river sections is realized for infrastructure construction or flood protection (Flatley et al., 2018). Ecological aspects need to be considered when planning river relocations, following the implementation of river protection regulations (e.g. the European Water Framework Directive, European Commission, 2000). River relocations therefore represent extreme cases within the restoration spectrum, and widely used concepts and strategies in river restoration are therefore applicable to river relocations (Wohl et al., 2005).

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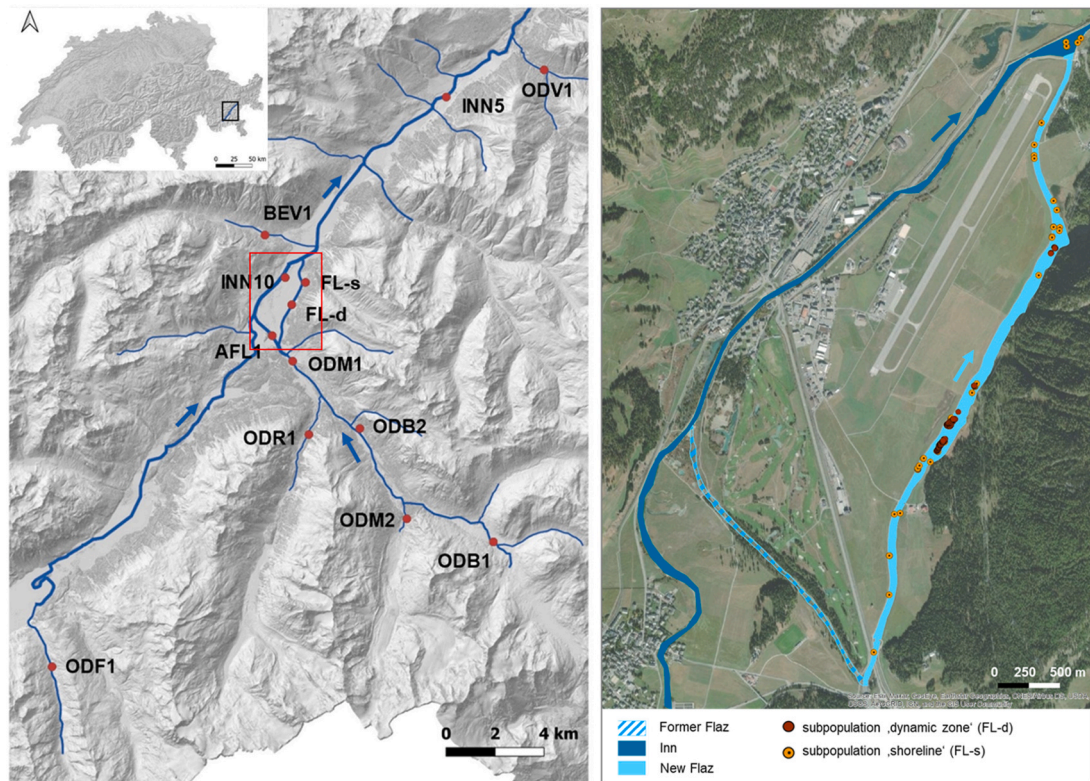


Fig. 1. Study site around the town of Samedan (Engadin, Switzerland), with location of the included *Myricaria germanica* populations along the Inn catchment (left). Blue arrows indicate flow direction. Abbreviations stand for the population ID (Table 1). The new Flaz was created in 2004 for flood protection and *M. germanica* plants (> 600 individuals, of which only a subset is shown as dots) colonized the whole river stretch (right): along the steep shoreline constructed of hydraulic blocks (orange dots) and on the gravel bars within the flow dynamics of the river (red dots; surface model of Switzerland: map.geo.admin.ch; aerial: ESRI base map). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Still, there are only few river relocation projects considering ecological aspects adequately (Flatley et al., 2018). A recent project shows positive effects on local biodiversity, as the new river section contained many natural structures and near-natural habitats (River Inde, Maaß et al., 2018).

There are several indicators for measuring river restoration success that can be used for evaluating the ecological value of relocated river stretches (Woolsey et al., 2007). The presence of typical floodplain species is a good indicator for the longitudinal connectivity and availability of near-natural habitat structures (Woolsey et al., 2007), and can consequently show the importance of the new river section within the whole river network. Additionally, presence of adults and juveniles indicate that habitat structures are suitable for species growth and reproduction, as well as seedling establishment, which is important for local persistence (Hale et al., 2019). This is particularly crucial for many sessile riparian plants within very dynamic riverscapes (e.g. alpine rivers) that form metapopulations to counteract dramatic loss of populations by natural hazards such as floods or drought periods (Mari et al., 2014).

Metapopulations consist of a network of colonized habitat patches allowing species to re-colonize new sites from source populations which might have been spared by extreme events. Genetic analyses allow to indirectly assess the connectivity of habitats and populations (here identified as spatially independent groups of individuals) within a metapopulation system (Fagan, 2002). While the genetic structure of populations along a catchment indicates if gene flow is ongoing or disrupted, comparisons of genetic diversity of various populations provide valuable information on the importance of individual sites (Hartl and Clark, 2007). It further shows if populations are more likely sources for other sites, or if they are sink populations that are not further contributing to gene flow between populations (Hartl and Clark, 2007; Tero et al., 2003). To maintain gene flow between populations, dispersal vectors, dispersal distances and also potential barriers to dispersal are critical entities to know. For many riparian species, adaptations to various dispersal mechanisms (e. g. Chen and Xie, 2007; Imbert and Lefevre, 2003; Reich, 1991), and the importance of upstream dispersal has been reported (Wubs et al., 2016).

We analyse the colonization processes of a characteristic riparian plant species, the German Tamarisk *Myricaria germanica* (L.) Desv. (Ellenberg and Leuschner, 2010) along a tributary of the river Inn in Switzerland. *M. germanica* is a flagship species for dynamic pioneer habitats and it is a key element of the habitat type *Alpine Rivers and their ligneous Vegetation with Myricaria germanica* (Code 3230, Directive 92/43/EEC by the Council of the European Communities, 1992). The species forms large metapopulations with fast colonization of new habitat sites to counteract losses through flooding. Therefore, their persistence depends on intact river dynamics,

including sediment transport, making it suitable and often used as indicator species for successful river restoration (Sitzia et al., 2016). Additional to its indicator value, its status as threatened in most European countries (Kudrnovsky, 2013) makes *M. germanica* an important species in several conservation programs along alpine rivers, mainly in terms of reintroductions (e. g. Italy: Michielon and Sitzia, 2015; Switzerland: Rieben, 2009; Austria: Schletterer and Scheiber, 2008; Germany: Woellner et al., 2019).

Our study profits from the unique opportunity to investigate the colonization of a relocated alpine river stretch of the river Flaz. The newly created stretch is ecologically designed to harbor dynamic zones allowing for the formation of gravel banks (Vonwiller et al., 2010), which provides habitat for pioneering species. After completion of the construction, the Flaz was indeed spontaneously populated by *M. germanica* and 14 years later, we studied the colonization process of the species including demographic and genetic aspects.

This study provides insight into the likelihood of the colonization of a non-natural river stretch by a plant species which is highly dependent on river dynamics. The analysis with variable microsatellite markers allows assessing founder events (reduced genetic diversity due to single individuals founding a new population; Templeton, 2008), and the role of metapopulation dynamics along the more stable shore-inhabiting individuals and the individuals on the gravel banks in the dynamic zone. Given the spatial proximity of additional populations along Inn and its tributaries and information on flood events, we trace the source for the recolonization of the new habitat.

We address the following questions: i) What is the demographic and genetic structure of the population at the relocated river Flaz? ii) Is the new population a sink or source for metapopulation dynamics in the catchment? iii) Are there single or multiple source populations based on genetic and demographic information? The results can provide insights into the connectivity along the catchment and reveal if the newly established population contributes to the metapopulation dynamics, by e. g. also playing an important role in subsequent colonization events of future restoration projects.

2. Material and methods

2.1. Study site

The study site is located at the river Flaz in south-east Switzerland in the region Engadin (9.884981, 46.526679, WGS84). The river Flaz flows from south to north over a length of 3.4 km and is a tributary to river Inn. The river section was created in 2003–2004 for flood protection measures around the town of Samedan (Fig. 1). The dynamic zone of river Flaz is separated from the surrounding pastureland by a solid and steep shoreline (hydraulic blocks) with height differences up to 2.5 m between water level and dam crest. After the restoration was terminated in 2004, a flood event ($130 \text{ m}^3 \text{ s}^{-1}$, mean frequency 10 years) supported the formation of particular intended structures in different sections of the Flaz (Vonwiller et al., 2010). After 14 years (2004–2018) the succession of the shoreline is dominated by bushes of *Salix spec.* and *Larix decidua*, dense tall herb stands (*Epilobium angustifolium*, *Lupinus polyphyllus*) and ruderal vegetation. Only the partially sandy gravel bars in the widening section are open sites in 2018 and host a few pioneer plants typical for alpine floodplains (e.g. *Gypsophila repens*, *Linaria alpina*).

2.2. Study species

The German Tamarisk, *Myricaria germanica*, is a perennial pioneer shrub growing on gravel and sand bars. It is the character species of the association *Myricario-Chondriletum chondrilloides* and *Salici-Myricarietum*, which can be found on alluvions along alpine floodplains that are frequently inundated and only sparsely vegetated (Leuschner and Ellenberg, 2017). The species of these communities are well adapted to periodically droughts and floods, and typical representatives are i.e. *Chondrilla chondrilloides*, *Dryas octopetala*, *Salix purpurea* and *Salix elaeagnos* (Kalmňková et al., 2021). Habitat availability for *M. germanica* is limited on the one hand by periodical flooding (sediment erosion and deposition) and on the other by proceeding succession in which the species is out-competed, mostly by dense willow shrubs (Sitzia et al., 2016). The turnover time of these habitats lies between 2 and 5 years for pioneer sites and 5–16 years for older gravel bars with shrubs (Rivaes et al., 2013). Therefore, *M. germanica* is dependent on intact river dynamics and is an appropriate indicator for near-natural river sites or restoration success.

M. germanica is widely distributed along braided rivers in central Europe and Asia (Schletterer and Scheiber, 2008), but underwent a strong decline due to habitat loss following hydro engineering, river channelization and gravel extraction (Sitzia et al., 2016; Werth and Scheidegger, 2014). Today, the species is listed as endangered in many European countries (national red lists, e.g. Metzinger et al., 2018; Niklfeld and Schratt-Ehrendorfer, 1999; Rossi et al., 2013). For Switzerland, *M. germanica* is listed as vulnerable in the national red-list (Bornand et al., 2016) due to its rapid decrease over the last century. Still, populations remained at a few catchments in Switzerland and display gene flow within and between sites (Werth and Scheidegger, 2014).

M. germanica germinates quickly (24–48 h after seed landing), shows early age flowering (1–2 years), and is reported to live up to 21 years (Kudrnovsky, 2013; Lener, 2011; Werth et al., 2014). The species shows adaptations (small seeds with pappus) to wind- and water-mediated dispersal (Bill et al., 1999, 1997), but especially wind dispersal is limited (Fink et al., 2017). Propagation via cuttings has proved to be successful (Koch and Kollmann, 2012) and therefore vegetative recruitment from drifted plants or plant parts is also possible. The plant is capable of selfing (Werth and Scheidegger, 2014), but pollination by insects has also been reported (observational data, Müller-Schneider, 1986; frequent visit of *M. germanica* by bees in Austria, Schiechl, 1957).

2.3. Population assessment

For assessing the colonization along the restored river site, the whole Flaz section was searched for *M. germanica* and every plant was mapped using GPS (Garmin Oregon 700). Plants were sampled along the shoreline (FL-s, see Fig. 1 and Table 1) and on gravel bars

Table 1

Sampling information and genetic diversity indices listed for the (target) Flaz population, also separately for the two subpopulations (FL-s, FL-d) and eleven natural populations within the same catchment area. Genetic diversity values were averaged over 19 microsatellite loci. Population ID, number of genetic samples (N), and mean statistics including number of different alleles per marker (N_A), allelic richness (A_R), observed heterozygosity (H_O), unbiased expected heterozygosity (uH_E), lat and long coordinates (WGS84) of the population locations are reported. The last line indicates the total values for the metapopulation (all individuals treated as one population).

Pop ID	River	N	N_A	A_R	H_O	uH_E	lat	long
FL	Flaz	147	2.368	0.182	0.040	0.184	9.884981	46.526679
FL-d	Flaz (gravel bar)	122	2.263	0.170	0.036	0.181	9.884981	46.526679
FL-s	Flaz (shoreline)	25	1.947	0.176	0.059	0.179	9.884981	46.526679
AFL1	Alter Flaz (Former Flaz)	3	1.211	0.133	0.035	0.091	9.874196	46.515531
BEV1	Beverin	41	1.526	0.152	0.034	0.153	9.871962	46.552636
INN5	Inn	40	1.632	0.154	0.045	0.154	9.970937	46.601308
INN10	Inn	3	1.632	0.028	0.000	0.028	9.881674	46.536374
ODB1	Ova da Bernina	20	1.684	0.226	0.037	0.187	9.988350	46.437050
ODB2	Ova da Bernina	39	1.474	0.137	0.022	0.137	9.919276	46.480341
ODF1	Ova da Fedox	9	1.263	0.086	0.018	0.086	9.751708	46.396107
ODM1	Ova da Morteratsch	22	1.632	0.185	0.029	0.173	9.884607	46.505902
ODM2	Ova da Morteratsch	40	1.526	0.115	0.038	0.115	9.942740	46.446552
ODR1	Ova da Roseg	41	1.368	0.128	0.008	0.128	9.892024	46.478693
ODV1	Ova da Varusch	38	1.474	0.135	0.024	0.135	10.02361	46.610131
Total		443	1.556	0.146	0.030	0.134		

within the dynamic riverine zone (FL-d, see Fig. 1 and Table 1). The individuals of both habitat types were further treated as two subpopulations (spatially subdivided group of individuals at the same location, but topographically distinguishable, Cronin, 2005).

To assess the population structure and better retrace of the colonization process, *M. germanica* plants were categorized in three age classes according to their contribution to metapopulation dynamics: class 1: < 1 year (0–10 cm), with a high mortality rate, class 2: 1–2 years old (11–50 cm), established young plants but not flowering and therefore not actively contributing to reproduction and dispersal and class 3: > 3 years (> 50 cm), plants with flowers, actively contributing with seeds to the population recruitment (modified after Lener, 2011). Field work and sampling was done from 18th–21st June and 23rd–25th July in 2018.

2.4. Genetic sampling along Inn catchment

For genetic analyses, 168 random samples from the population across the whole Flaz section were taken (age class 1: 39, class 2: 40 and class 3: 89 plants). Sampled leaf material was dried on Silica Gel (Silica Gel Orange, ROTH, product no P077.1) and subsequently stored at -20°C .

To assess the origin of the *M. germanica* population along the new river stretch, genetic data and samples of eleven potential source populations have been derived from an earlier genetic study on *M. germanica* in Switzerland (Werth and Scheidegger, 2014) including eight populations within the catchment of river Inn (BEV1, INN5, INN10, ODB2, ODF1, ODM2, ODR1, ODV1, see Table 1). Additional sampling in August 2019 of three populations upstream of the Flaz supplemented this study (AFL1, ODB1, ODM1).

2.5. Genetic analysis

To assess the genetic diversity of the population along the newly created Flaz river and to identify its potential source populations we used 12–18 mg leaf material of a total of 168 plants and carried out a microsatellite marker analysis. Similarly, 45 samples of three populations sampled in 2019 (AFL1: 3 samples, ODB1: 20, ODM1: 22) were analysed using the same protocol. Plant material was lyophilized (BETA 1–8 L0 plus, Christ, at 40 bar and -55°C) and total DNA was extracted using DNeasy®96 Plant Kit (Qiagen, Cat.No. 69181). Polymerase chain reaction (PCR) analyses for 22 microsatellite loci were performed following the protocol of Werth and Scheidegger (2011) using Multiplex PCR Master Mix, 2x (Qiagen, No. 1066295). After dilution (1:2) with ultrapure water, 1 μL was analysed with 9.5 μL HiDi-LIZ solution (Applied Biosystems, Lot. 1401295) and size standard mixture (concentration 15 $\mu\text{L}/\text{mL}$, GeneScan™ – 500 LIZ®, Applied Biosystems, Lot. 1401359) on a 3730xl DNA Analyzer (ABI, Applied Biosystems).

2.6. Data analysis

Taking into account morphological differences at river Flaz, we analysed the population along the new stretch as a whole and also divided the population into two subpopulations: same-aged old plants along the shoreline (FL-s) and age-mixed plants on the gravel bars within the dynamic zone of the river (FL-d, sediment relocation approximately every 5 years). These subpopulations were also analysed independently and checked for differences in genetic diversity, distance to other populations and clustering.

Fragment length was assigned using the software GeneMapper (Applied Biosystems, V5.0) and scoring bin sets of previous genetic analyses (Werth et al., 2014; Werth and Scheidegger, 2011, 2014). Raw genotype data has been formatted in Excel 2010 and the packages 'poppr' and 'tidyr' in R (R Core Team, 2019). Thresholds for missing data in the final dataset were as follows: < 40% missing data on average over all populations for single loci, and < 10% missing data for individual multilocus genotypes. Genetic diversity

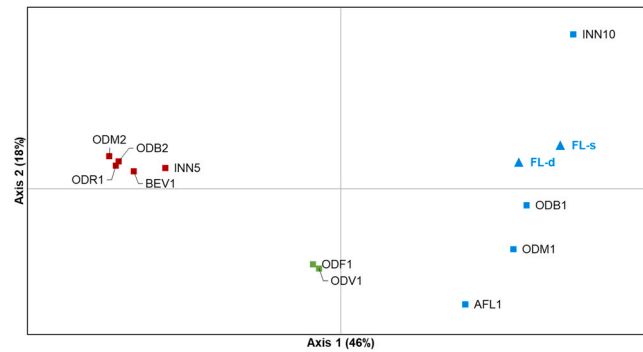


Fig. 2. Principal coordinate analysis of 11 populations along the Inn catchment and the two Flaz subpopulations (FL-s and FL-d, blue triangles) of *Myricaria germanica* within the study area based on the pairwise F_{ST} -values. Abbreviations stand for the population ID. The subpopulations at the relocated river Flaz (FL-s and FL-d) are most closely related to two populations further upstream (ODB1 and ODM1), as well as the geographically close populations at the former Flaz course (AFL1) and at Inn (INN10, clustering as group 1, all shown in blue). The other populations form two groups: group 2, geographically most distant from study site (ODF1 and ODV1, green squares) and group 3, all remaining populations within the metapopulation network (ODM2, ODB2, ODR1, BEV1, INN5, red squares, for details see text). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

estimates (number of different alleles per marker (N_A), allelic richness (A_R), observed heterozygosity (H_O), unbiased expected heterozygosity (uH_E), see Table 1) were analysed in GenAlEx 6.503 (Peakall and Smouse, 2006) and Arlequin 3.5 (Excoffier and Lischer, 2010). To check for population differentiation and source of variation a hierarchical analysis of molecular variance (AMOVA) and pairwise F_{ST} -values were calculated in Arlequin 3.5. The resulting distance matrix was used to gain a principal coordinate analysis (PCoA) with GenAlEx 6.503. We tested for isolation by distance (IBD) using Mantel-test for comparing genetic (F_{ST}) and geographical distance (GenAlEx 6.503). As geographical distance we used the distance between populations following the river course, calculated with ‘riverdist’ in R. We log-transformed the geographic distance and normalized the genetic distance ($F_{ST}/(1-F_{ST})$). To test for genetic structuring along Inn catchment, we used the Bayesian method ‘tess3r’ in R with 20 replicates for each of $K = 1:10$ (max.iteration=1000) under default settings considering population spatial distribution. Number of gene pools (clusters) were selected using the cross-validation function in ‘tess3r’. Genetic discontinuities among populations were displayed as changes in ancestry coefficients using Kriging interpolation.

3. Results

3.1. Population structure along Flaz

A total of 637 individuals of *M. germanica* have been mapped at the study site in 2018. The plants were distributed along the whole restored section with highest densities (94% of the population) on gravel bars within the active channel of the river (Fig. 1). The population at the Flaz consisted of about 65% very young (age class 1), 7% young plants (age class 2) and 28% reproducing individuals (age class 3, see Appendix, Fig. A1). Along the shoreline (FL-s) only old plants (age class 3) were found, while young plants only occurred on the sparsely vegetated gravel bars (FL-d). In the subpopulation of the dynamic zone (FL-d), 23% of the individuals were flowering and therefore reproducing, while 70% belonged to age class 1 and were still very sensitive to disturbance. Only 7% of the young plants could be designated as established (age class 2).

3.2. Genetic diversity at Flaz

Of the 22 microsatellite loci analysed, three had to be excluded, because of more than 40% missing data on average over all populations. Genotypes of 147 of the 168 samples taken in the field at the river Flaz showed less than 10% missing data and were therefore used for further data analysis.

The number of different alleles per marker (N_A) ranged from 1.21 (AFL1) to 2.37 (FL) and was highest in the Flaz population due to the larger sample size. Genetic diversity estimates (which can take values between 0 and 1) of the total Flaz population are generally low (<0.5) but high in comparison to all analysed populations of this study (Table 1), where highest diversity values are found in FL ($A_R = 0.18$, $uH_E = 0.18$), similar to populations further upstream (ODB1: $A_R = 0.23$, $uH_E = 0.19$ and ODM1: $A_R = 0.19$, $uH_E = 0.17$). For the unbiased expected heterozygosity, values were much higher than in other populations within the catchment (e. g. INN10: $A_R = 0.03$, $uH_E = 0.03$ and ODF1: $A_R = 0.07$, $uH_E = 0.09$ and AFL1: $A_R = 0.13$, $uH_E = 0.09$). Observed heterozygosity varied between populations from 0.0 (INN10) to 0.06 (FL-s), but was in FL (0.04) generally similar to the other populations (average over populations 0.03).

Genetic diversity parameters are similar between the two subpopulations within the Flaz (FL-s and FL-d), with a slightly higher N_A (2.26) and higher uH_E (0.18) for the plants within the dynamic zone (FL-d). Contrary to that, A_R (0.18) and H_O (0.06) were marginally higher in the shoreline subpopulation (FL-s). FL-s and FL-d were significantly differentiated ($F_{ST} = 0.064$, $p < 0.001$). The total Flaz

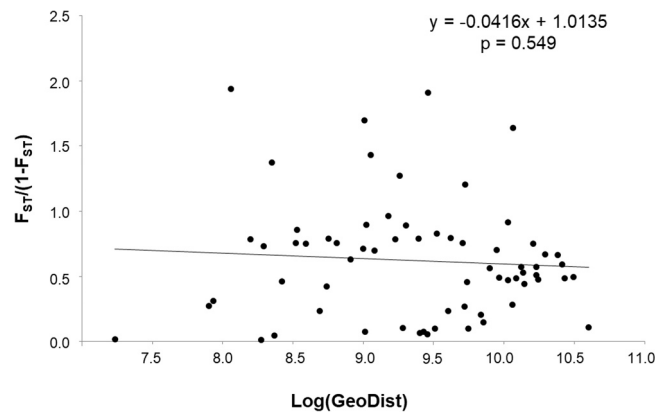


Fig. 3. Scatter plot of pairwise population genetic differentiation ($F_{ST}/(1-F_{ST})$) against logarithmic geographic distances ($\text{Log}(\text{GeoDist})$) among the populations of *Myricaria germanica* at the Inn catchment. Geographical distances are the distances between populations following the river courses, calculated with 'riverdist' in R. Mantel-Test reveals no isolation by distance ($p > 0.1$).

population shows lowest genetic distances to the closest population INN10 ($F_{ST} = 0.19$), to the upstream populations ODB1 ($F_{ST} = 0.19$) and ODM1 ($F_{ST} = 0.21$, Appendix, Table A1). Highest differentiation of the Flaz population was found to ODM2 ($F_{ST} = 0.47$) and ODR1 ($F_{ST} = 0.44$) both lying upstream to the new site. Average F_{ST} over all populations was 0.34.

3.3. Genetic structure of the metapopulation

The analysis of molecular variances on the newly established Flaz population and the potential source populations revealed a high amount of genetic diversity among individuals within populations (51%), followed by variance among populations (36%) and within individuals (13%, Appendix, Table A2). Mean pairwise F_{ST} between all populations ranges from 0.01 (ODB1–ODR1) to 0.59 (INN10–ODB2), indicating high variety in differentiation (Appendix, Table A1). Almost all pairs of populations show significant differentiation in F_{ST} values except six pairs: AFL–INN10, AFL–ODB1, AFL–ODM1, FLs–INN10, ODB1–ODM1, ODB2–ODR1. The population at the former Flaz stretch (AFL1) is not significantly differentiated from geographically close populations, contrary to the population at the new river site (FL), with exception of the non-significant differentiation between the shoreline plants of the Flaz (FL-s) and the geographically close INN10 (Appendix, Table A1).

The principal coordinate analysis with high support for the first axis (46%) revealed that the most closely related populations to the Flaz population (FL-s, FL-d) are originating from further upstream (ODM1, ODB1), and geographical quite close populations from the former Flaz course (AFL1) and the Inn (INN10, clustering as group 1 in blue, see Fig. 2). Two more groups are formed by the geographically most distant populations (ODF1, ODV1, group 2 in green, see Fig. 2) and all other populations up- (ODM2, ODB2, ODR1), and downstream BEV1, INN5) of the Flaz (group 3 in red, see Fig. 2).

There was no significant correlation between normalised pairwise genetic distances ($F_{ST}/(1-F_{ST})$) among populations and the logarithmic geographical distance along the river courses (Mantel-Test, $a = -0.04$, $r^2 = 0.005$, $p > 0.1$), indicating no isolation by distance within the studied populations (Fig. 3).

For the Bayesian inference of population clustering, the cross-validation score indicates three clusters within the Inn catchment. While cluster 1 (blue) and cluster 2 (yellow) are frequent in FL and INN10, cluster 3 (red) dominates ODB2, BEV1, ODR1, ODM2, INN5 (Figs. 4 and 5). In the most geographically distant populations, OVF1 and ODV1, are evenly assigned to clusters 1 and 3. AFL1, ODB1 and ODM1 show similar proportions of all three clusters. Both subpopulations within the Flaz population (FL-s and FL-d) show the same proportion of assigned genotypes to the three clusters (Fig. 5).

4. Discussion

4.1. Population dynamics along the new river

Fourteen years after the river relocation, *M. germanica* has colonized the whole stretch of the new river Flaz along the steep shoreline and on the gravel bars within the dynamic zone. The pioneer species forms a large population of more than 600 plants including various life stages, despite the semi-natural conditions with only a small active river channel missing lateral floodplain areas. As planned by hydraulic engineers, the alternating bars (Vonwiller et al., 2010) have proven to be suitable habitats and currently harbor 90% of the local *M. germanica* population. The ideal conditions in the dynamic zone close to the waterline allow for seed germination (Kudrnovsky, 2013) and explain the presence of mainly seedlings and young plants (70%). Nevertheless, juvenile plants are prone to erosion and since they are non-flowering, they do not yet actively contribute to the local gene pool.

While flowering and older plants are rare on the gravel bars, they are the only age class distributed along the shoreline: The 43 adult plants established between large rocks and dense vegetation, even along the channelized sections. These sites are not typical or known to be suitable for the species (Bill et al., 1997; Endress, 1975; Kudrnovsky, 2013), but provided a niche for the earliest colonizers of the

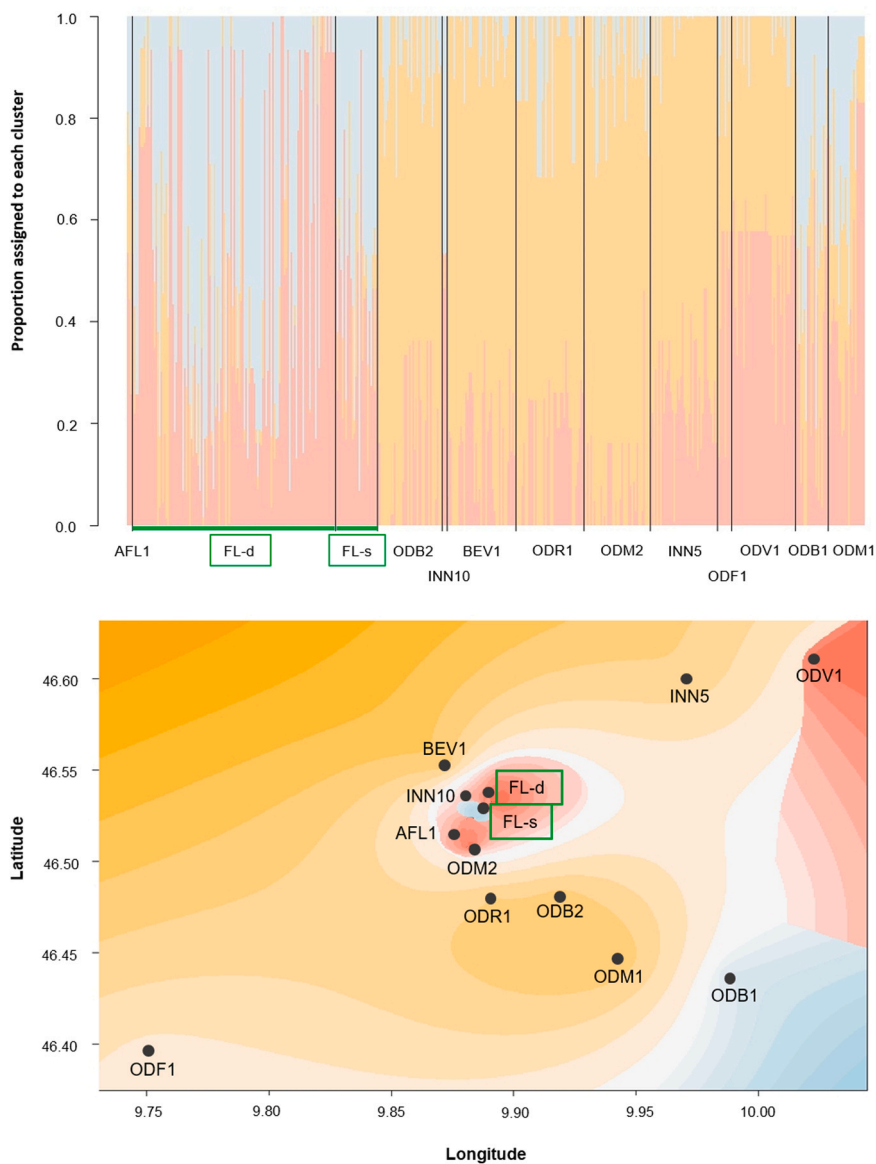


Fig. 4. Population structure analysis calculated with R package ‘tess3r’, assuming three clusters ($K = 3$, shown in blue, yellow and red), with bar plots representing admixture coefficients for each *M. germanica* individual (above) and spatial plot using Kriging interpolation (below). Abbreviations are population IDs (Table 1) and both Flaz subpopulations (FL-d, FL-s) are highlighted in green. Individuals of the subpopulations at the relocated river Flaz (FL-d and FL-s) show proportions of genotypes assigned to all three clusters (above), with a majority assigned to cluster 1 (blue). The individuals of the geographically close populations AFL1 and INN10 show similar patterns, while the other sites along the Inn catchment reveal that individual genotypes were mainly assigned to cluster 2 (yellow), with the exception of distant populations (ODB1: upstream of Flaz, blue; ODV1: downstream of Flaz, red, see above). While the spatial interpolation shows a continuum of the yellow cluster along the catchment, the pattern of the red and blue clusters is more complex (below). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

new river after the flood event in 2004 (frequency of occurrence every 10 years: $130 \text{ m}^3 \text{ s}^{-1}$, 8th/9th July 2004, see Janisch (2007)). These adult and flowering plants at sites protected from erosion form a good basis for the long-term persistence of the local population, providing a source of seeds for potential dispersal to the more dynamic gravel bars.

The shoreline individuals are of major importance to maintain genetic diversity along Flaz, as they show comparable diversity estimates to the subpopulation within the dynamic zone, despite the large size differences of the subpopulations. Contrary to that, the two geographically closest populations, one along Inn (INN10) and one along the former Flaz stretch (AFL1), also show small population sizes but have low genetic diversity (see Fig. 5). The high diversity of the few *Myricaria germanica* individuals along the shore is comparable to the genetic variability found in two large populations upstream (ODB1, ODM1, Fig. 5). Therefore, the colonized Flaz site is also an important source for gene flow among the populations at lower altitude in the Inn catchment.

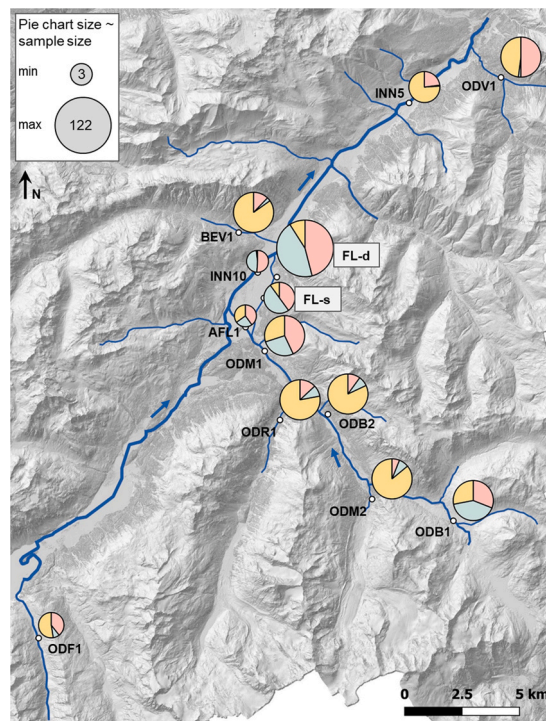


Fig. 5. Proportion of different genetic clusters within the populations derived from the population structure analysis calculated with R package ‘tess3r’. Size of the pie charts relatively reflects sample sizes. Both subpopulations of *M. germanica* at the relocated river Flaz (FL-d and FL-s) show the same proportions of assigned genotypes to the three clusters, with a majority assigned to cluster 1 (blue), also occurring in populations further upstream (e.g. ODM1, ODB1). While the frequency of individual clusters varies considerably between sites along the Inn catchment, both populations at Flaz and surrounding sites show high diversity with genotypes assigned to each of the three clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Metapopulation dynamics in the catchment: role of the new site

The relocation of whole riverine stretches mainly focuses on natural hazard prevention and land reclamation (Flatley et al., 2018), but also offer a unique opportunity to study population dynamic processes of typical riparian species. The river Flaz is centered in the Inn catchment, which shows low genetic diversity despite harboring many populations of *M. germanica* (compared to other catchments in Switzerland, Germany and Austria, see in Werth and Scheidegger (2014)). Nevertheless, the genetic diversity at the youngest site at Flaz is higher than the average genetic variability of all studied populations along Inn (see Table 1). Moreover, the two subpopulations at Flaz (shoreline and dynamic zone) are spatially and genetically different, similar to high genetic differentiation between most other populations in the catchment. Populations of *M. germanica*, as typical for plant species of the pioneer vegetation, are influenced by repeated extinction and colonization along catchments (Freckleton and Watkinson, 2002; Mari et al., 2014; Van Looy and Piffady, 2017). These metapopulation dynamics due to hydrodynamic events lead to genetic differentiation despite ongoing gene flow along a continuous river (meta-study by Honnay et al. (2010); see also for *Myricaria laxiflora*: Liu et al., 2006; Tero et al., 2003).

Although the Flaz population seems to be unique regarding the population structure (Figs. 4 and 5) it is closely related to other spatially close populations (AFL1, INN10, ODM1, see Fig. 2), but also to the farthest population upstream (ODB1). *M. germanica* is wind (Fink et al., 2017) and water dispersed (Bill et al., 1999; Werth et al., 2014), and genetic diversity structure can reflect these patterns. Additionally, pollen dispersal by insect pollinators can further increase genetic diversity (see also Hevroy et al. (2018), Müller-Schneider (1986)). The high genetic variance at the Flaz site as well as at the other Inn populations supports the influence of wind dispersal and pollination by insects over short distances. Long-distance dispersal by water is probably contributing likewise, given the absence of an isolation-by-distance pattern at the catchment scale (see Fig. 3).

The new site of Flaz with its large populations contributes to the genetic diversity in the catchment by showing a similar structure of various genotypes comparable to the most upstream population (ODB1, see Fig. 4). Given the high variability of the population in the dynamic zones as well as along the shoreline, the Flaz is not forming a sink population due to unidirectional downstream gene flow. Therefore, the new site can contribute to the maintenance of genetic diversity in the Inn catchment and might even play an important role in the colonization of future revitalized habitats in the area.

4.3. Single or multiple sources for the new river?

The similar age of the 43 adult plants along the shoreline provides a unique opportunity to reveal if the earliest colonizers of the Flaz originated from a single source. The comparable high genetic diversity of these individuals indicates that multiple sources – or multiple individuals as sources respectively – are more likely (see also the ‘migrant pool’ model by Slatkin (1977)). As genetically most similar populations are frequently most likely sources for new sites (see also Helsen et al. (2013)), we suggest that two populations upstream with similar genotype composition are likely candidates for sourcing the relocated Flaz river (ODB1 and ODM1).

As described above, the most likely event leading to the colonization of the shoreline population can be traced back to the flood towards the end of the relocation project at the site. Similar to findings of other studies, rare high flood events (frequency of occurrence every 10 years, similar to the flood in 2004 along Flaz) are more effective in dispersing seeds than frequent smaller floods (Hevroy et al., 2018). Additionally, the pioneer species are also adapted to vegetative dispersal, which allows for the spread of individuals over large distances by water (Nilsson et al., 2010; Werth et al., 2014). Therefore, multiple individuals or vegetative parts of individuals as sources but a single event are likely explaining the colonization of the restored Flaz shoreline.

The age structure of the subpopulation on the gravel bar with few older plants is more complex to trace to a single source or founder event. Additionally, the dynamic gravel bars were frequently changing over time: A colonization event is possible starting in 2008, when a flood ($38 \text{ m}^3 \text{ s}^{-1}$; frequency of occurrence every 5 years) reformed the gravel bars to their present shape (Pfuhlstein et al., 2012). Genetic similarity in the cluster proportions (Fig. 5) between the two subpopulations indicates that the shoreline plants are the most likely sources for the gravel bar subpopulation. Still, the other geographically close population at Inn (INN10) cannot be ruled out as a potential source, as it is not differentiated from the shoreline population.

Founder effects represented as limited genetic diversity due to the early colonization events were not detected for the Flaz populations (Figs. 4 and 5), similar to findings of other studies with varying levels of differentiation (Andersen et al., 2014; Antrobus and Lack, 1993; DiLeo et al., 2017; Helsen et al., 2013; Travis et al., 2002; Zucchi et al., 2018). Genetic diversity of riparian plant species along non-natural stretches might remain high if dispersal allows for gene flow between dynamic and altered habitats (e.g. for *Salix viminalis*: Mosner et al., 2012). This is likely also the case for the Flaz site, given the high genetic diversity, although the two subpopulations are genetically differentiated. The independent evolution results from ongoing gene flow in the younger gravel bar subpopulation, while there is no rejuvenation along the shoreline, where the subpopulations’ genetic structure still reflects the first colonization events.

Riparian plants are frequently adapted to wind- and water-mediated dispersal and additionally show vegetative dispersal, and are therefore able to spread in all directions (Nilsson et al., 2010; Wubs et al., 2016). Nevertheless, the fate of sessile plant populations on remote, restored and relocated sites can be threatened by subsequent loss of genetic diversity due to limited connectivity (e. g. orchid *Dactylorhiza incarnata* in an isolated reserve, see in Vandepitte et al. (2012)). The patterns of gene flow along the Inn catchment indicates connectivity between sites, but might also mask additional sources responsible for the earliest colonization events.

5. Conclusions

As a typical pioneer plant representative of the dynamic habitats along alpine rivers, *M. germanica* is particularly suitable for studying plant colonization processes and connectivity along the relocated river, especially by using genetic and population structure data. The results of the plants’ ability to re-colonize new habitat could be used as example for other species in the same habitat, and is important for nature conservation, particularly as *M. germanica* is a target in revitalization and reintroduction projects.

The turnover time of dynamic riverine habitats lies between 1 and 5 years for the pioneer stage and 5–20 years for older gravel bars, our study of a site 14 years after the relocation was able to provide information on the success of creating suitable pioneer habitats as well as the initiating and ongoing colonization processes. The time span was sufficient to allow deriving important lessons learned for river relocations and river restorations in general, and we suggest that similar time spans should be considered for success control of such projects.

Our results underline the importance of an intact metapopulation dynamic along rivers and especially ongoing connectivity. Different morphological structures in close spatial proximity within one location, e. g. steep shorelines, low shorelines and gravel bars, can host subpopulations from very different sources due to various dispersal events and dispersal vectors. Therefore, restoration planning should ensure that a mosaic of habitats is present at a relocated or revitalized river.

Particularly for sessile riparian plant species, extreme events such as large floods play an underestimated role in long-distance dispersal, as vegetative dispersal allows for multiple founders linked to one founder event. Consequently, successful river restoration by spontaneous population establishment of endangered species can only be achieved by maintaining or restoring flood dynamics within a river continuum.

This study shows that plants outside of regular river dynamics act as sources for habitats with shorter turnover times, where population rejuvenation takes place. Climate change scenarios assume an increase in frequency and intensity of flood events, stressing the importance of subpopulations outside the dynamic zone regarding fast recolonization of new habitats and maintaining genetic diversity. Therefore, riparian habitat diversity with low and high elevation zones along the shoreline should be a focus in river restoration, as the mosaic of habitats plays a crucial role for metapopulation dynamics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

See Fig. A1.

See Tables A1 and A2.

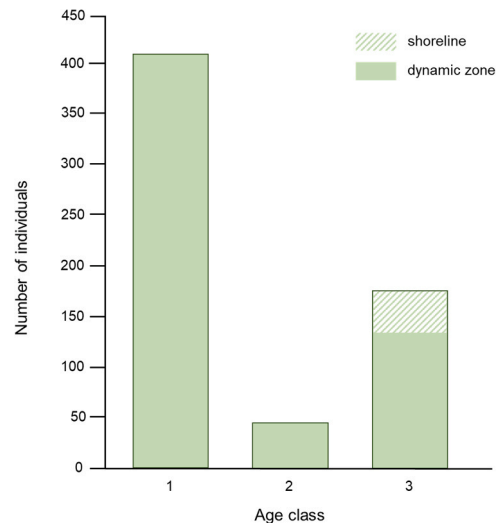


Fig. A1. Frequency distribution of the mapped *Myricaria germanica* individuals along the relocated river Flaz in the Swiss region Engadin among the three age classes (see text, modified after Lener, 2011). Most plants grow within the dynamic zone on the gravel banks, and only 6% of the population is found along the stable shoreline (striped bar) all belonging to age class 3.

Table A1

Pairwise F_{ST} -values between 13 populations of *Myricaria germanica* within the Inn catchment area in the Swiss region Engadin. Values and significance ($p < 0.05$; gray: not significant differentiation) were calculated with Arlequin 3.5. For the relocated river Flaz, two subpopulations FL-d (individuals on gravel bars within the dynamic zone) and FL-s (individuals along the shoreline) were analysed separately.

	AFL1	BEV1	FL-d	FL-s	INN10	INN5	ODB1	ODB2	ODF1	ODM1	ODM2	ODR1	ODV1
AFL1													
BEV1	0.39												
FL-d	0.25	0.45											
FL-s	0.24	0.46	0.06										
INN10	0.66	0.58	0.22	0.14									
INN5	0.45	0.09	0.43	0.47	0.56								
ODB1	0.09	0.41	0.21	0.15	0.21	0.43							
ODB2	0.43	0.06	0.44	0.48	0.59	0.13	0.42						
ODF1	0.48	0.34	0.31	0.36	0.62	0.33	0.33	0.32					
ODM1	0.02	0.41	0.23	0.19	0.32	0.44	0.06	0.42	0.33				
ODM2	0.49	0.09	0.48	0.52	0.66	0.22	0.46	0.04	0.40	0.47			
ODR1	0.43	0.07	0.45	0.50	0.63	0.17	0.44	0.01	0.36	0.44	0.07		
ODV1	0.36	0.31	0.32	0.39	0.55	0.30	0.37	0.35	0.10	0.33	0.40	0.36	

Table A2

Analysis of molecular variances (AMOVA) of 12 study populations of *Myricaria germanica* within the Inn catchment area in the Swiss region Engadin, calculated as weighted average over 13 (polymorphic) loci (Arlequin 3.5). The population of Flaz was treated as one population.

Source of variation	Sum of Squares	Variance components	Percentage variation
Among populations	639.28	0.83	35.85
Among individuals within populations	1144.31	1.18	50.99
Within individuals	134.50	0.31	13.16
Total	1918.08	2.32	100.00

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