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Conservation of the endangered *Myricaria germanica* (L.) Desv.: a keystone species of riverine habitats

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Conservazione della minacciata *Myricaria germanica* (L.) Desv.: specie chiave degli habitat ripariali

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Summary

Myricaria germanica (L.) Desv. is a pioneer shrub linked to natural river dynamics. Despite its high conservation and indicator value, there is a lack of information on factors affecting its population density and viability, and its long-term dynamics. The long history of river alteration has created novel systems with unknown dynamics, so population-level studies are necessary to understand, manage and restore *M. germanica*, preventing the loss of biodiversity associated to this keystone species. The main process that affects its populations is habitat fragmentation, especially in human dominated European rivers.

This thesis is based on a general review that deals with the distribution, biology and ecology of *M. germanica* (Paper I). Two research papers (Papers II and III) then concern the evaluation of *M. germanica* population-level long-term dynamics along a central eastern Alpine river (Trento Province, Italy) subject to human impact and lateral river corridor constraints. The success of a set of reintroduction projects in South Tyrol, a central eastern Alpine region, was also investigated through the collection of post-reintroduction population-level data. Lastly, a set of individual river basin traits data was collected in four north-eastern Italian basins and summarized, to complement the knowledge of this species biology. The last two topics are integrated into this main text.

Focusing on different time scales, due to the variability of riverine landscape contexts and on different spatial levels, from individual-, to river-, to regional levels, the overall goal of this work was to detect spatial and management components influencing *M. germanica* survival.

The analyses were conducted at European level (Paper I), on about 20 metapopulations distributed along a river basin (Papers II and III), 50 reintroductions were monitored (4,730 planted individuals), and traits were measured on 1,634 individuals. Papers II and III were written thanks to a collaboration with the University of Helsinki (Department of Environmental Sciences).

The data collection covered both species and environmental variables, considering current and historical field data and management variables of the surveyed river corridor and the surrounding basin-level asset. Regression models were used to relate species dynamics and traits to spatial, environmental and management variables. Descriptive statistics were used to summarize the morphological and chronological traits.

The approximately 150 literature sources for this species span four centuries, ten languages, and three continents, apart from the richness of biological and ecological data, they are full of forgotten information about the potential uses of this species (Paper I). Environmental site conditions (particularly active channel width) and management variables

have an impact on plant populations, the response of which however does not follow a clear spatial synchrony. This requires a long-term approach in studying population survival and a distinction between adults and juveniles (Papers II and III). Currently, reintroductions have had a mixed success, positive in specific locations, while the majority of individuals disappeared in the years following their planting. Morphological traits are characteristic of a short-lived shrub, but some long-lived individuals have been observed, usually away from rivers. Despite this, height, diameter and age were well correlated.

In general, the integrative method used allowed us to improve the knowledge about the drivers of *M. germanica* survival, the complex natural-human patterns and processes on different time-space scales that influenced population-level abundance and basin-level distribution.

Riassunto

Myricaria germanica (L.) Desv. è un arbusto pioniere legato alle dinamiche fluviali naturali. Nonostante il suo alto valore di conservazione e di indicatore, mancano informazioni sui fattori che influiscono sulla densità e vitalità delle popolazioni e sulle dinamiche a lungo termine. I nuovi sistemi fluviali, formatisi a seguito degli interventi umani, rendono necessari studi a livello di popolazione per comprendere, gestire, ripristinare *M. germanica* e prevenire la perdita di biodiversità associata a queste specie chiave. La frammentazione degli habitat rappresenta il principale problema per la sua conservazione.

Questa tesi si basa su un lavoro generale di revisione riguardante distribuzione, biologia ed ecologia di *M. germanica* (Paper I) e su due documenti di ricerca (Paper II e III) riguardanti la studio della dinamica di popolazione a lungo termine in un torrente alpino (Trentino, Italia), soggetto all'impatto umano e alle limitazioni delle aree laterali del corridoio fluviale. Inoltre, è stato studiato l'esito di una serie di reintroduzioni fatte in Alto Adige, attraverso la raccolta in campo, dopo la piantumazione, di dati a livello di popolazione.

Infine, in quattro bacini italiani nord-orientali sono stati raccolti dati sulle loro caratteristiche e riassunti, per integrare la conoscenza della biologia della specie. Gli ultimi due temi sono integrati nel testo principale.

Focalizzandosi su diverse scale temporali, per la variabilità del paesaggio fluviale, e diversi livelli spaziali (individuo, fiume e regione), l'obiettivo di questo lavoro è di rilevare le componenti spaziali e gestionali che influenzano sulla sopravvivenza di *M. germanica*.

Le analisi sono state condotte a livello europeo (Paper I) e su 20 metapopolazioni presenti in un bacino idrografico (Paper II e III). Sono poi state monitorate 50 reintroduzioni (4.730 individui piantati), e su 1.634 individui sono state misurate le caratteristiche morfologiche. I paper II e III sono stati realizzati in collaborazione con l'Università di Helsinki.

La raccolta dei dati ha riguardato sia la specie, che le variabili ambientali, considerando i dati attuali presi in campo e quelli storici, le variabili gestionali del corridoio fluviale esaminato e del contesto a livello di bacino fluviale. Sono stati usati modelli di regressione per mettere in relazione le dinamiche e le caratteristiche della specie con le variabili spaziali, ambientali e gestionali. Sono state eseguite analisi statistiche descrittive per riassumere i tratti morfologici e cronologici.

Sono state utilizzate circa 150 fonti bibliografiche, che abbracciano un arco temporale di 4 secoli e 3 continenti, scritte in una decina di lingue, e oltre alla descrizione biologica ed ecologica, sono ricche di informazioni sui potenziali usi che oggi sono stati dimenticati (Paper I). Le condizioni ambientali del sito (in particolare la larghezza del canale attivo) e i diversi tipi di gestione influiscono sulle popolazioni, la cui risposta tuttavia non segue una chiara

sincronia spaziale. È richiesto un approccio a lungo termine per lo studio della sopravvivenza della popolazione (Paper II e III) e una distinzione tra piante adulte e giovani. Attualmente, le reintroduzioni hanno avuto un successo alterno, positivo su specifici siti, negativo nella maggior parte degli impianti, scomparsi negli anni successivi alla loro piantumazione. I tratti morfologici sono caratteristici di un arbusto a breve ciclo di vita, ma sono stati osservati alcuni individui più longevi, di solito meno vicini ai corsi d'acqua. Nonostante questo, l'altezza, il diametro e l'età sono ben correlati.

In generale, il metodo integrato utilizzato ha permesso di migliorare le conoscenze sui driver della sopravvivenza di *M. germanica*, sui complessi schemi e sui processi naturali-umani, a diverse scale temporali-spaziali, che ne hanno influenzato l'abbondanza a livello di popolazione e la distribuzione a livello di bacino.

Contents

Appendix

Papers I-III

This thesis is partially based on the following papers, which will be referred to by their Roman numerals.

I. Michielon, B., Sitzia, T., 2018. Biological Flora of Central Europe: *Myricaria germanica* (L.) Desv.. *Manuscript*

II. Sitzia, T., Michielon B., Iacopino, S., Kotze, D.J., 2016. Population dynamics of the endangered shrub *Myricaria germanica* in a regulated Alpine river is influenced by active channel width and distance to check dams. Ecological Engineering 95: 828-838.

III. Sitzia, T., Michielon, B., Kotze, D.J., 2018. Plant population-level long-term dynamics: a case study of how a couple of years more could count. *Manuscript*

1. Introduction

Myricaria germanica, German tamarisk or False tamarisk (Deutsche Tamariske in German, Tamerice alpina in Italian), is a typical pioneer shrub on gravel bars in braided alpine rivers in the temperate zone of Europe and Asia. Over the past 150 years this species has suffered a dramatic reduction in Europe as a result of anthropogenic changes in watercourses. It is therefore a perfect indicator of natural rivers, but its survival is also possible along regulated rivers, the crucial limiting factor being the absence of natural disturbances that might drive primary succession.

Since the long history of riverine landscape alteration in Europe has created novel populations with unknown dynamics, long-term studies are necessary to understand, manage and restore human dominated landscapes, preventing the loss of keystone species like *M. germanica* (Essl, 2013; Kudrnovsky, 2013a; Kudrnovsky, 2013b).

Thus, together with resource management, land use planning and other broad-scale environmental issues, population-level studies might also provide a scientific basis for **biodiversity conservation**, clarifying the relationship between riverine landscape pattern and ecological processes (Turner, 1989). Indeed, landscape can be defined by two strictly related components: **structure and function** (Figure 1). Landscape structure (or pattern) is the spatial relationship between landscape elements or patches, while landscape function (or process) is the interaction between these spatial elements (Hobbs, 1997). Lastly, **landscape change** is the alteration in structure and function occurring over time.

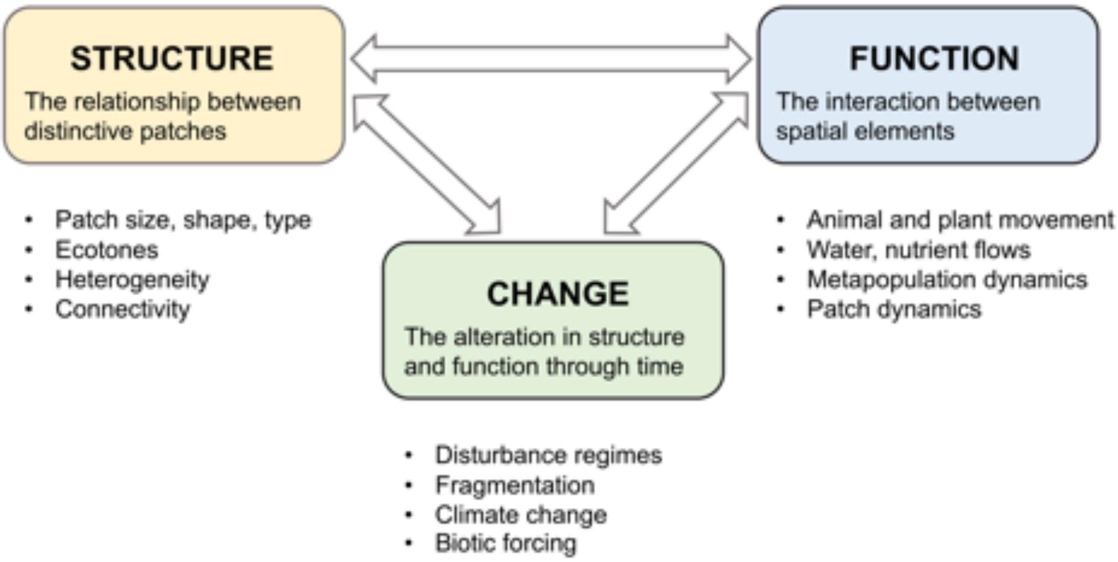

Figure 1. Landscape ecology key components and their main study objectives. From Hobbs (1997), modified.

Individual-level traits are also fundamental as indicators of biodiversity response to landscape change. Simple morphological attributes (i.e., life-history traits) combined with suitable establishment and environmental conditions, are the most important drivers of colonization success. Such attributes are often helpful for identifying successional stages (Schwienbacher et al., 2012). Indeed, integration between the available trait databases, and databases that combine species abundance with environmental information, can help to identify the traits that respond to, influence or interact with environmental factors and ecological processes (Suding et al., 2008), a major field of functional ecology (McGill et al., 2006).

Databases of plant traits such as LEDA (Knevel et al., 2003), TRY (Kattge et al., 2011) or BIOPOP (Poschlod et al., 2003) are very useful since they provide possible determinants of the response of primary producers to environmental factors, and how they can affect other trophic levels, ecosystem processes, services and diversity. While they are rich in information for many keystone tree and herbaceous species, they can be scanty for minor species like *M. germanica*. It is therefore necessary to measure traits on a large number of individuals from different sites to provide additional predictors for *M. germanica* survival.

Survival of *M. germanica* might rely either on existing populations, with natural regeneration, or on planted individuals. Indeed, one of the emerging tools in the biological management of ecosystems is the reintroduction of locally extinct or endangered plants, even though they are in their natural habitat. Despite the large number of reintroduction projects carried out, the choice of the most appropriate method remains controversial and must be assessed separately for each species (Fahselt, 2007). For example, it is necessary to decide whether to use seeds, young seedlings, adult plants or clonal propagation material (Whisenant, 1999). However, it is often difficult to experimentally monitor the success of reintroduction projects, because it is difficult to obtain the original information about the type of project, type of material, number of individuals introduced, method of introduction and interventions in the field.

1.1. Habitat ecology of *Myricaria germanica*

Myricaria germanica (Figure 2) is a habitat specialist, light-demanding pioneer species depending on unstable, open habitats with a high proportion of fine sand, sufficient water supply for seed germination and low to moderate river dynamics (Karlsson, 2010; Kudrnovsky, 2013a; Müller, 1998; Werth et al., 2014).

It is an explicitly light demanding species, which is unable to grow on shady sites and in willow stands can only be found at their edges (Bill et al., 1997). Its strategy is to thrive in harsh riparian habitat conditions, instead of competing with other species for favorable environments (Kudrnovsky and Höbinger, 2015).

Figure 2. ***M. germanica*: A) parts of the flowering plant: the leaves are flat, narrow and alternate; B) Flowering shoot: tip of the long shoot with the terminal inflorescence and underlying enrichment shoots; the latter arise from scale-shaped bracts; C) part of the peduncle 1) short stemmed single flower with bract; the 5 lineal, about 3 mm long sepals are membranous at the edge; the 5 petals are pink or white, about 4 mm long; 2) flower in longitudinal section with the narrow pyramidal ovary; 3) flower after removal of calyx and petals: the outer 5 of the 10 stamens are longer than the inner 5; the anthers are purple to red; 4) cracked capsule fruit; 5) seeds with the stalked hair; 6) cut longitudinally-elongated seeds. From Thomé (1905).**

M. germanica is a flagship and keystone species for natural dynamic riparian habitats. It is the characteristic species of the European Union habitat 3230 "Alpine rivers and their ligneous vegetation with *Myricaria germanica*" listed in Annex I of the Habitats Directive 92/43/EEC, of which the overall conservation status is considered unfavorable-bad (Halada, 2017).

Its narrow ecological niche lies between the "ability to survive" in highly dynamic sites marked by substratum structures and the massive competition suffered by this pioneer species when it is overgrown by shading willows and alders (Goster et al., 2017).

According to the classification by Grime (1979), *M. germanica* is a "stress tolerator" and a "stress-strategist", adapted to a lack of nutrition and temporary water shortage, which is driven out by competition (Müller, 1995).

Figure 3. ***M. germanica*** **inflorescence (Avisio River at Ziano di Fiemme, 960 m a.s.l., Trento, 25/07/2009).**

Its traits are highly suitable for colonizing and growing on river gravel or sand bars, provided that they are temporarily and periodically flooded (Prach, 1994). The main habitat limitations are due to the inability of the species to compensate for the high relocation frequency by appropriate colonization of new areas, and this suggests that their survival strategy is geared more to persistence of once-occupied sites, than to the permanent occupation of new land (Bill et al., 1999). More rarely it colonizes secondary sites such as landslides and debris flows (Michielon and Sitzia, 2014), moraine deposits at glaciers, solifluction slopes, lake shores and pebbly sea-shores (Karlsson, 2010; Petutschnig, 1994), road embankments, dams and gravel-pits (Karlsson, 2010), and industrial wasteland (Rostanski and Wozniak, 2000). It is rarely grown for ornament but may escape from gardens in a few localities where it might be regarded as an alien species, like in Denmark and Southern Sweden (Hultén and Fries, 1986). According to the authors' observations, soil types are mostly sandy or gravelly, alkaline, with low nitrate and phosphate delivery, even though the species tolerates acidity and a high organic matter content, showing a wide adaptability to different soils.

1.2. Plant community description

The phytosociological indicator value of *M. germanica* poses some problems. It can be found within different phytosociological orders and associations. According to the syntaxonomical framework proposed by Mucina et al. (2016), *M. germanica* occurs as a young plant in the *Epilobion fleischeri* alliance (class *Thlaspietea rotundifolii*) and as a pioneer plant on river alluviums of the *Salicion eleagno-daphnoidis* alliance (class *Salicetea purpureae*). The associations belonging to the *Epilobion fleisheri* of which *M. germanica* is one of the characteristic species are *Epilobietum fleischeri* Frey 1922, *Myricario-Chondrilletum* Br.-Bl. in Volk 1939 and *Epilobio-Myricarietum germanicae* Aichinger 1933 (Grabherr and Mucina, 1993). In Mediterranean Europe, *M. germanica* is also a characteristic species of the *Andryaletum ragusinae* Rivas Br.-Bl. et O. Bolòs 1958 (Rivas-Martínez et al., 2011). The *Salici purpureae-Myricarietum germanicae* Moor 1958 is the only association belonging to the *Salicion eleagno-daphnoidis* of which *M. germanica* is a characteristic species.

Across its European range, accompanying species pools vary considerably (Essl, 2013), the common species associated with *M. germanica* within different communities are: *Achnatherum calamagrostis*, *Agrostis gigantea*, *Anthyllis vulneraria* subsp. *alpestris*, *Calamagrostis epigejos*, *Calamagrostis pseudophragmites*, *Campanula cochleariifolia*, *Campanula cochleariifolia*, *Chlorocrepis staticifolia*, *Dryas octopetala*, *Epilobium fleischeri*, *Epilobium dodonaei*, *Equisetum palustre*, *Erigeron acris* subsp. *angulosus*, *Erucastrum nasturtiifolium*, *Festuca arundinacea*, *Gypsophila repens*, *Hieracium piloselloides*, *Hippophae rhamnoides, Juncus alpinoarticulatus*, *Juncus articulatus*, *Juncus bufonius*, *Linaria alpina*, *Phragmites australis*, *Poa alpina*, *Poa nemoralis*, *Chondrilla chondrilloides*, *Populus nigra*, *Salix daphnoides*, *Salix eleagnos*, *Salix nigricans*, *Salix purpurea* ssp. *gracilis*, *Salix triandra*, *Sesleria albicans*, *Thymus praecox* and *Typha minima* (Grabherr and Mucina, 1993).

Kudrnovsky (2013a) distinguishes three main groups and 12 subgroups within the *Salici purpureae-Myricarietum germanicae* in the Eastern Alps, this confirms the wide variability of this association. Moreover, in a recent study, Kudrnovsky and Kalníková (2015) have described nine groups of indicator plant species which represent variations of the *Salici-Myricarietum* vegetation structure according to different site conditions, as follows:

- from lowland to higher altitudes: *Salix eleagnos*, *Salix purpurea*, *Alnus incana*, *Agrostis stolonifera* agg., etc.;
- lowland floodplains: *Salix alba*, *Populus nigra*, *Epilobium dodonei*, etc.;

- floodplains in medium and higher altitudes: *Poa alpina*, *Anthyllis vulneraria* agg., *Epilobium fleischeri*, *Saxifraga aizoides*, etc.;
- fresh and moist conditions: *Deschampsia cespitosa*, *Saxifraga aizoides*, *Carex flacca*, *Carex flava*, *Juncus articulatus*, etc.;
- alkaline fens: *Tofielda calyculata*, *Poa farinosa*, *Poa palustris*, etc.;
- lime rich floodplains: *Sesleria caerulea*, *Dryas octopetala*, etc.;
- pioneer sites: *Tussilago farfara*, *Chlorocrepis staticifolia*, *Epilobium dodonei*, *Campanula cochleariifolia*, *Gypsophila repens*, etc.;
- alkaline floodplains: *Aster alpinus*, *Oxytropis campestris*, etc.;
- more stabilized conditions: *Larix decidua*, *Alnus incana*, *Picea abies*, *Pinus sylvestris*, etc..

M. germanica is also a characteristic species of the European Union habitats 3210 "Fennoscandian natural rivers", 3220 "Alpine rivers and the herbaceous vegetation along their banks", 3230 "Alpine rivers and their ligneous vegetation with *Myricaria germanica*" and 3250 "Constantly flowing Mediterranean rivers with *Glaucium flavum*" (European Commission, 2013).

1.3. *M. germanica* life cycle

1.3.1. Plant development and longevity

The initial stage is the most critical in the life cycle of this plant (Lener, 2011). The length growth of the long shoots ends no later than the death of the terminal fruit stands. At this time, however, secondary thickness growth has not yet been completed. Below the main flower stand, the long-wheel drive lignifies and can produce new long-tines next year (Opitz, 1993). *M. germanica* produces a remarkable amount of infructescences, and the number of seeds rises exponentially with plant size (Lener, 2011). The fruiting and flowering season lasts from May-June to August-September, but variations are possible according to the site altitude and water supply over the growing season (Bachmann, 1997; Kudrnovsky, 2002). Normal initial maturity age for *M. germanica* is 2-3 years (Bill, 2000; Lener et al., 2013). This is influenced by the period of more or less early germination and by more or less favorable environmental conditions.

Due to the river dynamics and also overgrowth by taller-growing species, individuals are generally no older than 20-30 years (Kudrnovsky and Höbinger, 2015), most frequently about 10-15 years (Ellenberg, 1996; Kudrnovsky, 2002). Schweingruber et al. (2007) measured an average age of 7.7 years at the Morteratsch glacier foreland, at 1900-2100 m a.s.l..

Figure 4. A 40-year old plant of *M. germanica* which is growing in a currently arid area (Biotop Prad, 880 m a.s.l., Prad am Stilfserjoch, South Tyrol, 25/07/2017).

The maximum age of plants is subject to local and temporal variability. The death of individuals or at least the death of plant parts is probably genetically determined (Schweingruber et al., 2007), but the maximum age limits are changed and modified by local conditions.

In the last decades many river beds have been excavated with the consequent lowering of the ground water by a few meters and the original riparian habitat, without river dynamics, has become a dry habitat in which *M. germanica* can survive longer. Recruitment is impossible, but the reduced competition from other shrub-tree species allows *M. germanica* to survive longer than expected (Ellenberg, 1974). In fact, a few 40-year-old plants have been observed growing at Prad Biotope, a site that became arid, along Solda River, at Prad am Stilfser Joch, South Tyrol, Italy (Figure 4).

1.3.2. Seed dispersal

Seed lightness makes them predestined for a long-range dispersal by wind (Lanz and Stecher, 2009), but dispersal by water is also possible (Figure 5) (Bill et al., 1997).

Figure 5. ***M. germanica*** **flowers are insect-pollinated, and are aggregated in racemes that bear up to 100 flowers. The germination rate is high, but short in time. However, seeds can be transported by water over long distances, despite the rather short floatability and germination rate reduced in time (Sulden River at Sulden, 1865 m a.s.l., Stilfs, South Tyrol, 23/07/2013).**

Propagation by wind can take place upstream or downstream (Werth and Scheidegger, 2014) until distances that are not exactly proportional to wind speed. The majority of seeds fall next to the plants, but distances of up to 25 m have been recorded at a wind speed of 1.9 km/h (Lanz and Stecher, 2009). Maximum distances of 50-100 m have been reported (Bill et al., 1997; Fink et al., 2017) using water-filled trays (Stöcklin and Bäumler, 1996) and, occasionally, a dispersal distance of several kilometers is possible (Bill, 2000). For example, a recent natural site was found 10 km from the nearest population (Fruscalzo, 2012). Between 3,300 and 3,500 seeds/m^2 have been found close to the tamarisks, but 400-600 seeds/m^2 can still be found at 90 m (Lener et al., 2013). The seed rain of a *M. germanica* population is extraordinary high (Müller and Scharm, 2001) and Lener (2011) measured a maximum seed pressure of about 500,000 seeds/m^2 (17/07/2010) (Figure 6).

Diaspores can also float, so they can be dispersed by water (Bill et al., 1997). Seeds are able to reach suitable new habitats thanks to "water" transport (Bill et al., 1997; Lanz and

Stecher, 2009). It is possible that seeds can be transported by water over long distances, despite the rather short floatability and germination rate reduced in time.

Figure 6. ***M. germanica*** **opening fruits with seeds (Avisio River at Ziano di Fiemme, 960 m a.s.l., Trentino, 26/07/2013).**

1.4. Response to abiotic and biotic factors

Climatically, *M. germanica* is best suited to continental and mountain zones. The frequency and intensity of floods and droughts that characterize the habitat are the most important disturbances to which the species responds. The limiting factor for seedling survival is a **sufficient water supply**. When the groundwater surface beneath the gravel sinks tamarisks suffer from water deficiency and slowly die. Lowering of the groundwater has a greater effect than a lack of precipitation during the vegetation period (Opitz, 1993). However, in dry conditions, more root biomass is produced, preferentially fine rather than structural roots, with the aim of developing the rhizosphere and maximizing water collection; this is combined with a reduction in aboveground biomass, thus reducing evaporation (Lavaine et al., 2015). This is coupled with the ability to store water in leaves (Kammerer, 2003).

M. germanica is dependent on fluvial dynamic sites (Figure 7), which are always free from disturbing competitors, although lacking special adaptations to resist flooding at the physiological level (Kerber et al., 2007).

Long term studies of aerial photos and recently done population studies at the diverted reach of the Isar River (Reich et al., 2008, Harzer et al., 2018), high lighten the importance of extraordinary floods (of the century) for population dynamics of *M. germanica* in diverted river stretches.

Figure 7. Gravel bars recently developed on the Mareit River, after ecological restoration (2009-2011) and *M. germanica* reintroduction with a lot of new *M. germanica* seedlings (Stanghe, 955 m a.s.l., Sterzing, South Tyrol, 17.07.2017).

Injured and gravel covered plants can sprout repetitively within a few weeks (Bill et al., 1997). Bent-down branches can also re-root and cross through a layer of gravel and sand, up to 20-25 cm thick, **sprouting** again after only two weeks (Figure 8) (Bill et al., 1997), even long shoots lying in the water and covered by substrate can form roots (Opitz, 1993).

Figure 8. *M. germanica* is dependent on fluvial dynamic sites, which are always free from disturbing competitors, although lacking special adaptations to resist flooding at the physiological level (Biotop Sanderau, 1450 m a.s.l., St. Jakob im Pfitschtal, Pfitsch, South Tyrol 18/07/2015).

M. germanica is firmly anchored in the substrate with its far-reaching roots and can also colonize coarse-grained sites in groundwater connection. It is classifiable as moderately flooding-sensitive. Flooding of its rhizosphere induced slight decreases in net photosynthesis at an external partial pressure of CO_2 of 35 Pa within the first 10 days. 35 days after flooding it reached only 55% of the level of unflooded control plants. There was no recovery of gas exchange after flood termination. Vitality, rejuvenation and density of individuals of *M. germanica* are significantly lowered in these areas.

M. germanica is **shade intolerant**, which is why it is outcompeted by species growing in more stable environments, like willows and alders (Bill et al., 1997). Because the species is weak in competition there is a strong need for recurring disturbances for establishment. The significance of submersion and therefore of flood events is not only the recruitment of new individuals, but also that almost all competitors do not survive this or their abundances are at least kept low (Bill et al., 1997).

In general, *M. germanica* does not develop dense vegetation canopies (Kudrnovsky, 2015). The average density of plants is around 5/100 m^2, the maximum known size of a population is 8,500 with local density of a maximum 100 juveniles or 10 adults/m^2 and 100% canopy cover (Sitzia et al., 2016). In such conditions, intraspecific competition may cause a decrease in the proportion of individuals.

Herbivory by mammals is known for the snow leopard (*Panthera uncia*), where entire droppings have been composed of tamarisk and up to 41% contained twigs 2-4 cm long (Mallon, 1991). The leopards have seen feeding deliberately on the plants, particularly during the mating season (Chundawat and Rawat, 1994). Potential, but tentative explanations for this behavior are roughage, digestion, anti-parasite and supplemental diet (Sunquist and Sunquist, 2002). Wild ungulates and livestock have also been occasionally observed feeding on twigs.

Several **insects and mites** (e.g., Curculionidae, Eriophyidae, Gelechiidae, Itonididae, Momphidae, Psyllidae, and Tortricidae) are host specific to Tamaricaceae, sometimes cause galling and bud teratisms (Kovalev, 1995). The insects that are closely related to *M. germanica* are: *Coniatus tamarisci* (Fornasari, 1997), *C. repandus* (Fornasari, 2004), *Merulempista cingillella* (Robineau, 2011), *Istrianis myricariella* (Huertas-Dionisio, 2012), and *Diorhabda elongata deserticola* (DeLoach et al., 2003). The dipter *Egle concomitans* (Pandelle, 1900) is a probable depositor of eggs that develop into larvae who feed on seeds (Opitz, 1993), like *E. myricariae* (Grossmann, 1998).

More than 50 **fungal taxa** may be unique to *Tamarix* species, among these there are possibly approximately 5-10 unique fungal species for each species (Thambugala et al., 2017). Although specific data for *M. germanica* are not available, a close species, *M. laxiflora*, hosts

26 genera of endophytic fungi classified into 5 subphyla, 7 classes, 12 orders, 17 families (Tian et al., 2015) and present dark septate fungal associations (Zhao et al., 2016). Arbuscular mycorrhizal fungi are one of the most widespread types of symbiotic associations, but very few studies have been conducted in riparian transitional zones between aquatic and terrestrial ecosystems (Zhao et al., 2016), including *M. germanica*, which, to date, lack any investigation, but we expect that they could be present to resist stressed environments.

2. Structure, focus and goals of the thesis

This thesis is based partially on one review (Paper I) and two research papers (Papers II, III) on the evaluation of plant species biology, ecology and population-level dynamics in fragmented habitats. The success of a set of *M. germanica* reintroduction projects and morphological traits were also investigated and are integrated into this main text.

I. Michielon B., Sitzia T. (2018) Biological Flora of Central Europe: *Myricaria germanica* (L.) Desv. *Manuscript*

II. Sitzia T., Michielon B., Kotze D.J. (2016) Population dynamics of the endangered shrub *Myricaria germanica* in a regulated Alpine river is influenced by active channel width and distance to check dams. Ecological Engineering 95: 828-838.

III. Sitzia T., Michielon B., Kotze D.J. (2018) Plant population-level long-term dynamics: a case study of how a couple of years more could count. *Manuscript*

Focusing in each paper and in the main text on different specific objectives due to the variability of riverine landscape context and habitat type, **the overall goal of this thesis was to detect spatial and management components influencing *M. germanica* survival**. Overall, the studies considered both the **population** (with current and historical field data) and **individual level** (collecting morphological and chronological characteristics that could influence population dynamics along a river).

Specifically, we investigated:

(a) the available information on the biology of *M. germanica* growing in Central Europe (Paper I);

(b) factors that affect the long-term population dynamics and viability of *M. germanica* (Paper II);

(c) if integrating the time series of population data could change the results of the objective b) (Paper III);

(d) the determinants of the success of reintroduction projects, given by the post-plantation establishment of viable populations (main text);

(e) whether a difference in the *M. germanica* traits existed among three rivers having different bio-climate, geology and fluvial morphology affected by different intensities of anthropogenic disturbance (main text);

(f) the total size of and the factors that affect the population abundance of *M. germanica* at a regional scale (main text)

As Wu and Hobbs argued (2002), although diverse theories and methodologies exist, effectively integrating human-related processes into ecology may remain one of the ultimate challenges for ecologists. **Through the different tools and methodologies used, we wanted to demonstrate the notable information that a keystone species like *M. germanica* might provide both in theory and practice.**

The following sections of the thesis contain a resumé of the methodologies and results for the aspects investigated; within brackets the papers are referred to for insights and fuller explanations.

3. Methods

3.1. Study areas

The research studies were conducted in northern-east Italy, i.e. in the Trento province (Paper II and III) and Trentino-Alto Adige region, Belluno and Udine provinces, as shown in Figure 9.

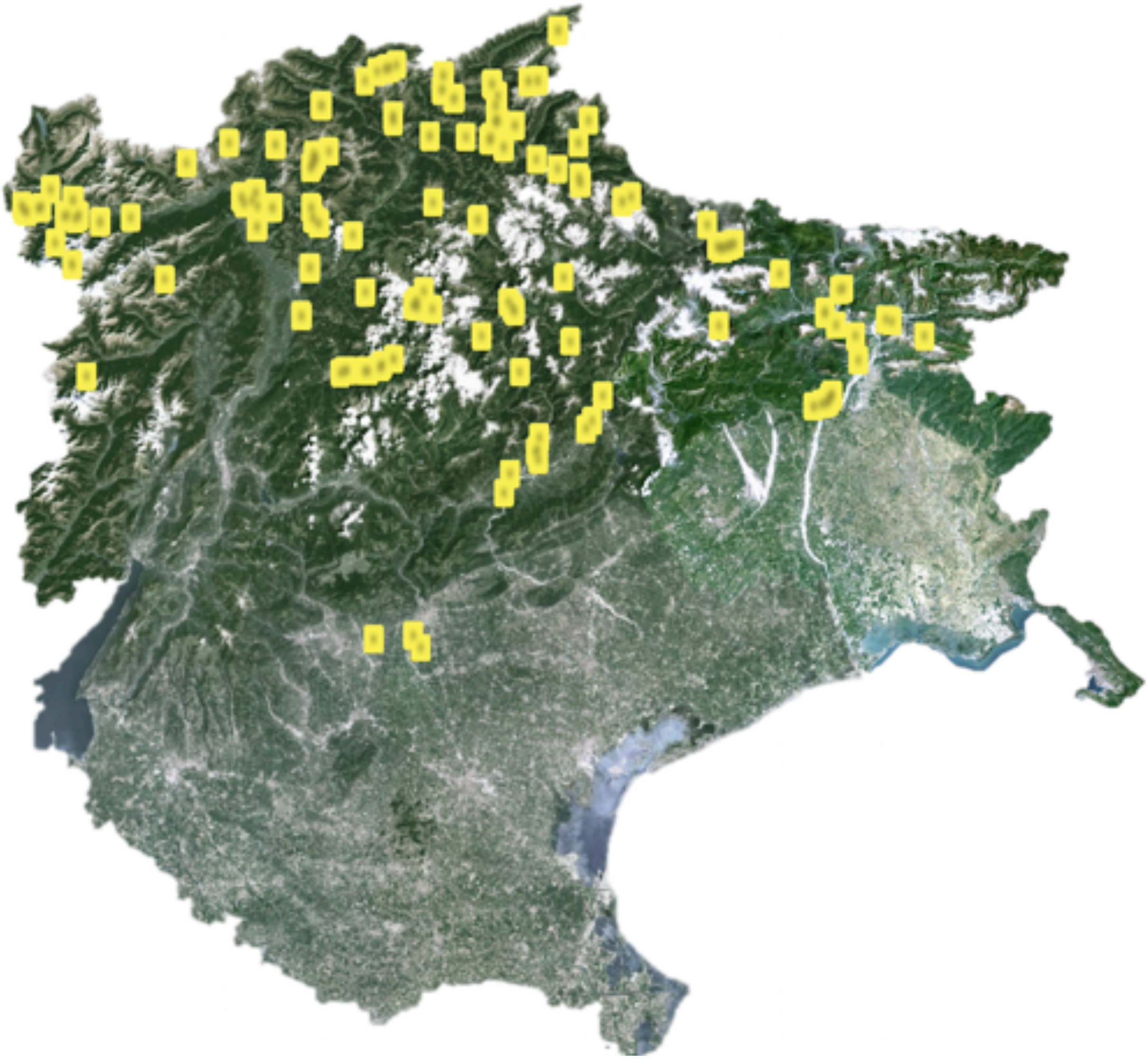

Figure 9. The 161 *M. germanica* sites (including extinct sites) visited in the field in south-eastern Alps in north-eastern Italy.

The analyses were conducted at the scale of one single river, i.e. Avisio River (Paper II and III), and considering the Adige, Piave, and Tagliamento Rivers together (Table 1). The first three rivers are highly impacted by humans, the last is more left to spontaneous evolution. Brenta River was also visited, but populations of *M. germanica* were not detected there and are most probably extinct.

Table 1. Number of sites with presence of *M. germanica* and extinct for river basins

Number of naturally regenerating sites	**Sites with *M. germanica***	**Sites extinct**	**Tot.**
Adige River basin (Provinces of Bozen and Trento)	40	33	73
Plantations in Adige River basin (Province of Bozen)	14	20	34
Brenta River basin and a near small basin (Provinces of Vicenza and Padova)	0	3	3
Piave River basin (Provinces of Belluno and Udine)	19	9	28
Tagliamento River basin (Province of Udine)	19	4	23
Total	92	69	161

The review paper covered researches conducted on *M. germanica* populations in Europe and the world (Paper I) (Figure 10).

Figure 10. The country of authorship of the literature review sources.

3.2. Data collection and elaboration

As reported in the § 2, the research for the three papers was conducted at population, individual and regional level, considering current and historical field data of the surveyed habitat and the analysis of the general conditions of three river basins: Adige, Piave and Tagliamento.

3.2.1. Population-level

At population-level, we collected a set of environmental data, using field observations, cartographic and aerial photographic sources and other databases. Altitude was measured from a digital terrain model. Two fundamental geomorphological variables, active channel width and river corridor width, were measured from aerial photos. Some anthropogenic river works were detected. Active channel width was defined as the wetted boundaries of the maximal flood, typically covered by gravel, and river corridor width as the boundaries of the plant communities growing near the river, influenced by river dynamics; the presence, on both banks, of river protections, and the fact that these were made with cemented boulders, were considered indicators of anthropogenic disturbance; distance of the site centroid to the nearest upstream and downstream check dams was used to quantitatively assess the influence intensity of check dams.

We determined past and current population site length parallel to the river, past and current area occupied by the population, presence of site in 2000, regeneration of site after 2000, population extinct, population extinct by direct human action and population density were used to characterize each population and as indicators of more natural conditions. The occurrence of protected areas was used as indicator of institutional efforts Table 2). The number of adult plants, able to bloom, and the number juvenile plants, immature individuals not yet blooming, were used as response variables in the analyses (Papers II and III).

Table 2. Explanatory variables collected at population-level.

Environmental variables	Species variables
altitude (m a.s.l.)	past population site length measured along river (m)
floods number per year	past area occupied by the population (m^2)
active channel width (m)	current area occupied by the population (m^2)
active river corridor width (m)	current population site length measured along river (m)
boulder riverbank protection	population density (plants/100 m^2)
riverbank protection on both sides of the river	presence of site in 2000
concrete riverbank protections	regeneration of site after 2000
check dam presence	population extinct
sediment storage area	population extinct by direct human action
distance of the site centroid to the nearest upstream check dam (m)	protected area (%)
distance of the site centroid to the nearest downstream check dam (m)	population living along water course
sediment size	planted population

3.2.2. Reintroduction success

The factors determining the success or failure of *M. germanica* plantations were investigated in Bozen province. The possible post-plantation conditions are: planted site disappeared, planted site still existing without juveniles, planted site still existing with juveniles. Either the success or failure of a plantation can depend on many factors, such as the type of project, type of material used, number of individuals introduced, method of introduction, and interventions carried out on the field.

The agency responsible (see acknowledgements) of Bozen Province provided a list of plantations of *M. germanica*. For each plantation site, the list reports the name of the site, planting year, number of plants, and name of the site manager. From 1999 to 2018, 4,730 tamarisks were planted during 57 interventions performed in 44 sites.

We georeferenced the plantation sites (Figure 11), if necessary, asking the site managers where exactly the tamarisks had been planted. The managers mostly replied by sending orthophotos, highlighting the plantation site, along with some notes. Only a few plantation sites were not recovered. The field surveys were preceded by a literature search concerning projects and hydraulic interventions carried out by the division in the last decades or under implementation in South Tyrol.

The abundance of *M. germanica* was measured, counting or visually estimating the number of adult and juvenile plants. We investigated the possible causes for the success or failure of the plantation and the relationships between presence of the species and other natural and anthropogenic factors, and future prospects. Field surveys were performed in summer over several years, from 2013 to 2018.

The search for tamarisks was often difficult. The plants found were often short, had slow growth, few branches and small and green-yellow leaves rather than glaucous, poor flowering, and were often suffocated by the more luxuriant surrounding vegetation.

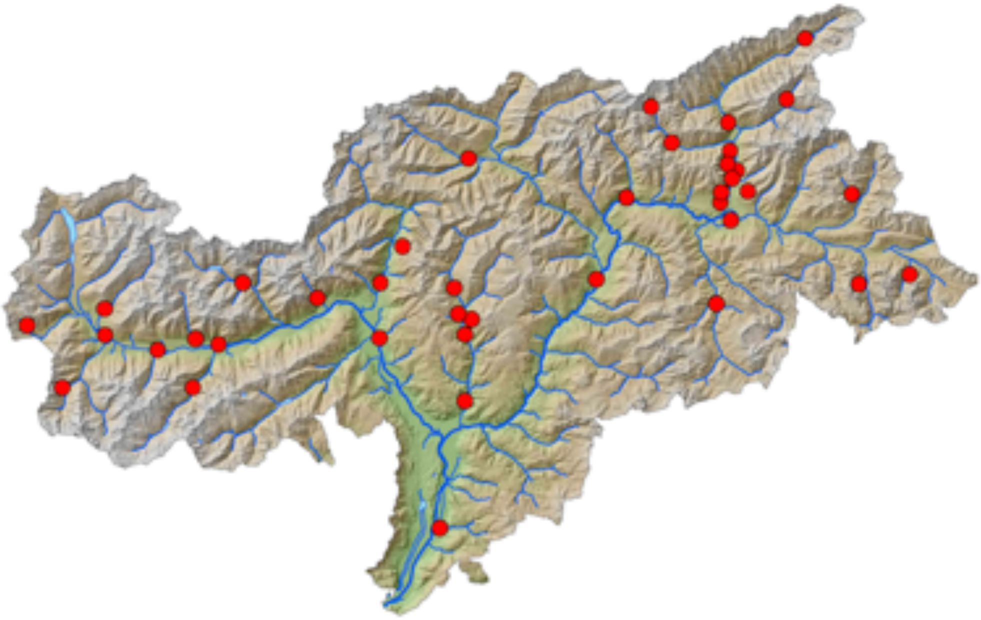

Figure 11. Reintroduction sites of *M. germanica* in the Province of Bozen.

3.2.3. Individual-level

At the individual level, on a random sample of 30 adult plants maximum (where available) per site, we measured the height of the plants, total number of branches, diameter of the largest branch and number of inflorescences. In addition, on a random sample of 5 adult plants per site, the largest branch of each plant was cut and used for age determination. A 1-cm thick cross section of the branch was prepared and smoothed, and observed under a stereoscope. Annual rings were counted.

Figure 12. A viable population of thousands of *M. germanica* plants on Tagliamento River at Tolmezzo (Udine Province) in a dynamic natural site (360 degree panoramic photo, 15/10/2017).

3.2.4. Basin-level

We investigated the differences between three basins in the distribution of plant traits. Where present, these differences were commented on in relation to the characteristics of the basins. The three basins are all located in north-east Italy and are briefly described below (Figure 13).

The **Adige River** rises near Resia Lake at an elevation of 1586 m a.s.l. and ends in the Adriatic Sea. The main stream is 409 km long and drains a catchment of 12,149 km^2. The river basin contains 550 lakes of glacial origin, most of which have a surface of less than 1 ha (Autorità di Bacino del Fiume Adige 2008). The geological characteristics of the Adige basin were defined during Alpine orogeny. For the overlapping of different rock complexes it is possible to distinguish three main groups or zones: Pennidic, Austroalpine and Southern Alps (Autorità di Bacino del Fiume Adige, 2008). More recent deposits can be found on the valley floor.

The climate in the Adige River basin is characterized by dry winters, snow and glacier-melt in spring, whereas it is humid during summer and autumn. Annual average precipitation values range between 500 mm and 1600 mm. The Adige River basin presents a summer flood dominated system with a strong glacial/snowmelt influence (Chiogna et al., 2016). Water management for hydropower production is performed with 28 reservoirs, 34 large hydropower plants (Autorità di Bacino del Fiume Adige, 2008) and more than one thousand small hydropower plants. The basin is also intensively exploited by a large number of small withdrawals associated to a variety of water uses: agricultural, civil and industrial.

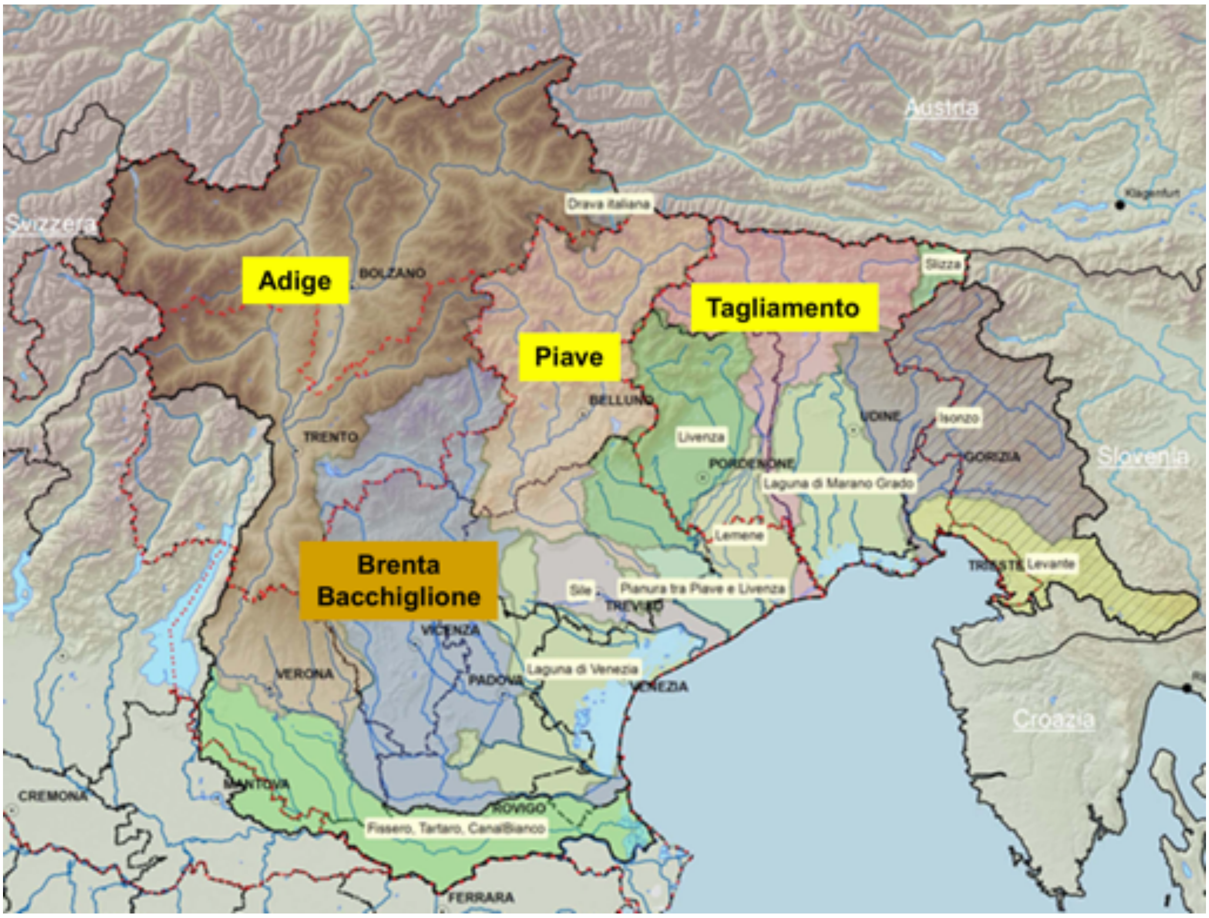

Figure 13. The river basins of the Triveneto area, River basin district of the Eastern Alps (source: Autorità di Bacino Distrettuale delle Alpi Orientali).

The **Piave River** flows, from its source at 2037 m a.s.l., for 222 km to the Adriatic Sea with an average slope of 0.004 m m^{-1}. The drainage basin has an area of 4022 km^2 and is composed mainly of sedimentary rocks. Morphologically, the river can be divided into an upper, middle, and lower course. The upper course, where the river is generally incised in bedrock and therefore has a quite narrow channel, the middle course, where the river is very wide and characterized by a multithreaded channel pattern, the lower course, where the river meanders have been artificially straightened in places (Surian, 1999). Despite a centuries long history of conflicting water uses, especially in the last century the Piave River basin has experienced a rapid increase in human exploitation of its water resources that followed the construction of a series of dams and reservoirs built along its main stream and most important tributaries from 1930 to 1960.

Nowadays there are 13 major reservoirs, mainly used for hydropower production, and a number of diversions and other regulating hydraulic devices that contribute to the management of river flows in the mountain range of the Piave basin.

The temporal evolution of the discharge, downstream of major regulation devices, is strongly influenced by the reservoir operations and their underlying management criteria. The complexity of the system is increased by the parallel presence of an artificial hydraulic network carrying significant flows. This utilization artefact is superimposed on the natural river network to serve as a link among the various reservoirs and energy production sites.

A significant part of the discharges originating from the Piave catchment is diverted from the watershed to the outer Livenza River basin by a pumping system located next to the S. Croce Lake. The impacts of agricultural use and hydropower management are greater than civil and industrial uses. The dynamic behavior of the water exploitation system in the Piave River basin causes dam-induced alterations of the natural streamflow regime (Figure 14).

Figure 14. A viable population of thousands of *M. germanica* plants at Santa Maria delle Grazie (Alleghe/San Tommaso Agordino, Belluno Province), 970 m a.s.l., on Cordevole River, Piave Basin, in a sediment storage area upstream of Alleghe Lake (360 degree panoramic photo, 02/08/2017).

The **Tagliamento River** is considered one of the few European gravel-bed rivers with high ecomorphological complexity and dynamics (Tockner et al., 2003). It therefore constitutes an invaluable resource as a reference ecosystem for the Alps and as a model ecosystem for large temperate rivers. The Tagliamento River flows unimpeded by high dams, from 1192 m a.s.l., to the Adriatic Sea, for 178 km with a slope varying in the range 0.003-0.005 m m^{-1}. The drainage basin has an area of 2743 km^2 (Surian et al., 2015).

The human impacts on the river are water abstraction and gravel exploitation. Water is abstracted for hydropower generation in the upper area. Nevertheless, large tributaries are characterized by a natural flow regime, in addition, the flood dynamics of the main stream of the Tagliamento is largely unaffected by water abstraction. The Tagliamento River corridor has escaped massive river engineering and floodplain development schemes and is morphologically intact along virtually its entire length.

The corridor thus retains the functional characteristics of a near-pristine system: strong longitudinal, lateral and vertical connectivity, high habitat heterogeneity, and a characteristic sequence of geomorphic types and very high biodiversity (Tockner et al., 2003). The riparian corridor, about 150 km^2 in length, excluding tributary corridors, consists of five major landscape elements: surface water, bare gravel, vegetated islands, riparian forest and topographical low areas that are unforested. The active zone of the Tagliamento River reaches a maximum width of about 2 km in the upper part of the coastal plain section. In some reaches the river divides into more than 10 channels with a maximum shoreline length of 22 $km \cdot km^{-1}$ (Tockner et al., 2003).

The complex downstream variability in river discharge and sediment transport regimes, local hydraulic conditions, and the materials within which the channel has formed have resulted in a high diversity of geomorphological styles of river platform along the corridor. It preserves natural dynamics with flooding, the major physical disturbance along river corridors, and smaller and frequent water level fluctuations, important for creating and maintaining habitat heterogeneity. In unconfined floodplain sections, maximum annual amplitudes of surface water levels are about 2 m (Tockner et al., 2003).

Mean annual precipitation in the Tagliamento basin is approximately 2000 mm, ranging from 1500 mm up to 3100 mm. Seasonal maxima in precipitation as well as in river flow occur in autumn and spring, whereas minima are observed in winter (Surian et al., 2015). The Tagliamento River is characterized by a flashy pluvio-nival flow regime, which results from both Alpine and Mediterranean snowmelt and precipitation regimes.

3.2.5. Regional-level

The regional-level analysis includes all the spontaneous population sites surveyed.

3.2.6. Statistical methods

The information from geographical data (geo-referenced) is managed through the use of GIS software and their extensions (QGIS and ESRI ArcGIS). Remote sensing data (aerial photographs, maps), hydrological data (precipitation, flow, floods, etc.) and spatial planning data (settlements, land use, roads, etc.) have been analyzed.

Moran's I was used to test whether there is spatial autocorrelation between sites within the same year. The null hypothesis is that abundance values are randomly distributed across the study area.

Variability in abundance of adult plants was checked to find any auto- and cross-correlation in space and time. Spatial synchrony refers to coincidental changes in abundances or other time-varying characteristics of a geographically-disjunct population and its existence may be due to dispersal, dependence of population dynamics on synchronous stochastic effects, and trophic interactions with other species. The absence of such synchrony between nearby populations is a signal that they do not fluctuate simultaneously and some populations are likely to be abundant. This is very important for conservation because some population sites might serve to re-establish declining populations (Liebhold et al., 2004). Existence of spatial synchrony was researched using a Mantel correlogram for multivariate data sets (multi-year observations per site) and its statistical significance via Monte Carlo randomizations, following the procedure described by Gouhier and Guichard (2014). The Mantel correlogram shows how correlated pairs of spatial observations are when the distance (lag) between them is increased. Here it was created by computing the correlation between the time series of pairs of sites as a function of the lag distance that separates them (Gouhier and Guichard, 2014). The number of lag classes, in which the maximum distance between sites is divided, was set to have at least one site in each class.

To evaluate the effects of geomorphological and anthropogenic variables on abundance, Generalized Linear Mixed Models (GLMMs) were used, and a negative binomial error distribution of the abundance data was assumed. Two models were performed, one on adult plants and one on the juveniles. Site was added as a random factor to account for repeated measures (i.e. sampling the same site over time).

All predictor variables were considered in these models. However, due to the extremely clumpy nature of the data and the complexity of the models, these variables were evaluated as follows. A base model was constructed including year as a fixed factor and site as a random factor. One predictor variable was then added at a time and its significance was evaluated. Altogether, distinct models, for adult plants and juvenile plants, were constructed, with each model including year, site (as a random factor) and one of the predictor variables. Results were presented for the effect of year (irrespective of its significance) and the significant predictor variables.

The function Moran.I in package ‘ape’ (Paradis et al., 2004), for spatial autocorrelation within year, the package ‘synchrony’ (Gouhier and Guichard, 2014), for spatial synchrony analysis, and the function glmer.nb in package ‘lme4’ (Bates et al., 2015), for the GLMMs, were used, all executed using the R statistical software (R Core Team, 2018).

The analyses of the reintroduction success are descriptive and aimed to check the establishment of populations after planting.

We used histograms to discover, and show, the underlying frequency distribution (shape) of the set of traits data. This allowed the inspection of the data for its underlying distribution (e.g., normal distribution), outliers, skewness, etc. We also reported the main statistical indicators for each trait. Moreover, we applied linear mixed-effects models to test the relationships between pairs of traits, where a causal relationship was considered possible. Site was added as a random factor with the function lmer in the package ‘lme4’ (Bates et al., 2015).

We used boxplots to graphically depict groups (river basins) of traits data through their quartiles. Box plots also have lines extending vertically from the boxes (whiskers) indicating variability outside the upper and lower quartiles. Outliers were plotted as individual points. We also used linear regression to model the relationship between the river basin and one or more traits (or independent variables).

We analyzed the relationships between environmental attributes of each spontaneous population site (explanatory variables) and the abundance of *M. germanica* adults and juveniles (response variables) with the data collected in 2017. These data are available for the entire study region, for a total of 131 sites. We included also extinct sites, where the abundance is 0. The regression models are the same as those used in Paper II, but without a random effect (no replicated measurements over several years). To compare the means between basins, we applied a Tukey post-hoc test with the function glht of the package 'multcomp' (Hothorn et al., 2008).

4. Main results and discussion

Regarding the analysis of the population-level approach, we refer to the full papers reported in the appendix. The following results concern the **reintroduction success, individual-, basin-, and regional-levels** analyzed through the methods explained above (§ 3.2).

4.1. Reintroduction success

The populations of *M. germanica* can be preserved in the long term only by enhancing or re-naturalizing the habitats. The dynamic processes of solid material deposition and hydrological balance must be restored (erosion, sedimentation, flooding). Re-naturalization can achieve significant results also by the integration of environmental policies of soil protection and recovery of natural areas, restoring environmental and biocenotical characteristics, as well as ecological functionality.

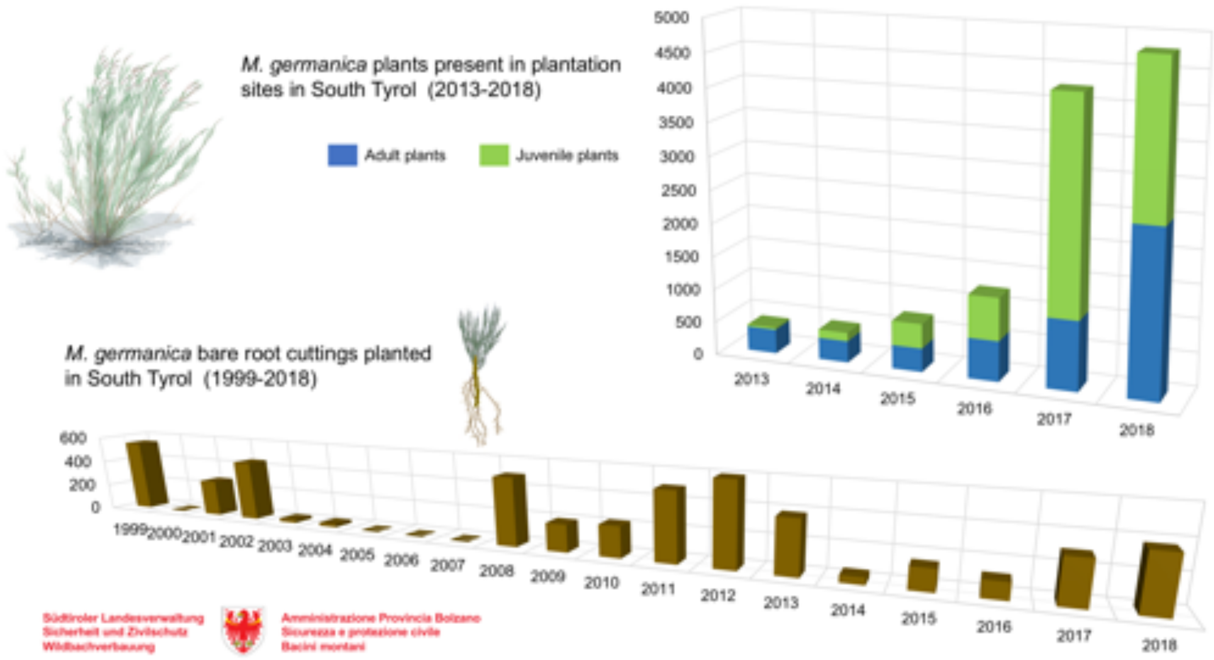

Figure 15. Bare root cuttings planted in South Tyrol from 1999 to 2018 (on the bottom) and plants present in plantation sites from 2013 to 2018 (at the top).

The results are positive in 4 sites, and negative in all the others (Figure 15), some sites are still present, even if not regenerating.

Terrestrial riparian habitats are characterized by disturbances that follow each other with different frequencies and intensities. To be populated by the communities of characteristic species, the habitats must be available and connected in a spatio-temporal way. Such habitats cannot be stored in a static way, but must be continually recreated by the dynamics of outflow and transport of solid materials, in particular by floods. Major floods remodel sections of the riverbed by modifying its morphology, destroying existing habitats and creating space for new ones. From an ecological point of view the dynamics of a watercourse is considered sufficient when it creates the whole variety of typical habitats and species communities. In most watercourses this has been reduced by construction interventions, aggregate withdrawals and outflow regulation measures (Werth et al., 2011).

Many terrestrial species, especially those living on sand and gravel bars, such as *M. germanica*, base their survival on a periodic return of disturbing factors, such as floods. If these events do not occur, the sediment bars are populated by willow bushes and in the long run they turn into flood plains and consequently the species typical of primitive environments disappear.

The decisive factor for the protection of *M. germanica* is the restoration of appropriate habitats. To do this, two different strategies can be followed: firstly, the creation of very large dynamic sites, with large populations, in a water network system that tolerates the natural partial loss of the population caused by floods, or the creation of small habitats with regulated and limited substrate dynamics, to avoid the total loss of smaller populations. This means that man, through planning and design techniques, can create habitats where he can reduce stress caused by natural floods, to prevent the total loss of smaller populations (Wittmann and Rücker, 2006).

When is a reintroduction successful? According to Primack and Drayton (2012) "it can be said that a reintroduction is really successful only when a population increases in number and expands the area of presence, the plants reach the flowering and the fruiting, it gives rise to a second and third generation of plants, and the population provides indications that will persist in future decades. Another success is when the population disperses the seeds in the surrounding areas and forms satellite populations". In the floristic mapping of Germany, for example, plants are established if they occur in the area for at least 25 years and spontaneously reproduce (Harzer et al.x, 2018).

In recent years studies have been conducted on different propagation methods and reintroduction projects for *M. germanica*, particularly in Austria (Latzin and Schratt-Ehrendorfer, 2005; Wittmann and Rücker, 2006; Egger et al., 2010; Kammerer, 2003; Feichtiger and Gumpiger, 2012), also in Germany (Koch and Kolmann, 2012) and Switzerland (Rieben, 2009). Attempts to reintroduce have not always succeeded and often the entire planted contingent has been removed by a single flood event. It is not entirely clear when and how recovery actions are actually useful or effective (Kammerer, 2009).

The results of the reintroductions depend on numerous factors, often differing from site to site, and it is not always possible to generalize. In any case, it should not be forgotten that the reintroductions of *M. germanica*, even if they fail, can promote a certain popularity in public opinion, an important factor for active conservation measures (Wittmann and Rücker, 2006).

Based on a negative binomial regression we can verify that the number of juveniles still living in plantation sites is positively correlated to the active channel width ($p < 0.0001$). However, we should consider that the count outcome is over-dispersed: the main effect here is due to one single site (Ratschings, Sterzing) which has about 3,000 juveniles and > 60 m of active channel width.

The results of reintroductions carried out in South Tyrol are briefly summarized below.

The most positive intervention is the one in Ratschings, on the Mareit River. The main reason for the success is the size of the intervention, on a 2 km long stretch and with a considerable enlargement of the river corridor. The intervention approaches a true restoration or re-naturalization and the conditions of fluvial dynamics present should allow the future survival of *M. germanica*. This at the moment seems to be a successful reintroduction.

As for the Ahr River, various plantations have disappeared, with the exception of those in Gatzaue, Gais, where there has also been a renewal of the species. This indicates that Gatzaue can be a favorable site, and one could think of extending the area and type of intervention to have an adequate widening of the riverbed and conditions of river dynamics. The disappearance of the other sites, probably due to erosion of the shore, seems to indicate that, despite the enlargements made in single stretches, the river corridor is still limited and there are no sand and gravel bars favorable for the establishment of *M. germanica*.

The analysis of the results of reintroductions in South Tyrol indicates that the favorable conditions for the establishment of *M. germanica* require well-structured and integrated projects, substantial interventions, over several years, in which to restore the indispensable river dynamics conditions for the renewal of the species. The results of small and limited interventions remain uncertain.

In general, it can be concluded that in order to achieve positive results in reintroductions, these aspects should be taken into account:

- a careful design;
- choice of the most suitable sites;
- removal of the causes of the extinction;
- use of appropriate propagation material, i.e. container rooted cuttings or seedlings (Figure 16);
- planting of plant material;
- registration of the plantation site location;
- conducting periodic monitoring of the establishment;

- determination of the causes of success / failure;
- recording and publication of data;
- dissemination, education and awareness raising.

Figure 16. ***M. germanica*** **1-year old bare root cuttings, not the most appropriate plant material for reintroductions.**

4.2. Individual-level

A total of 1,634 plants were sampled, 782 in the Adige basin, 455 in the Piave basin, 397 in the Tagliamento basin, for a total of 85 sites. The ages of 382 branches sampled were counted. The results are summarized in the histograms reproduced on the following page.

Before looking at the graphs, we must remember that the age was measured on the largest branch. Some plants were uprooted and their age measured at the real base of the plants. Thanks to this, we were able to check the existence of a positive and significant linear relationship between branch and plant age, and between branch and plant diameter (Figure 17).

Age plant = 1.47 Age branch - 0.42 ($R^2 = 0.76$, $p < 0.0001$)

Diameter plant = 5.36 + 1.38 Diameter branch ($R^2 = 0.72$, $p < 0.0001$).

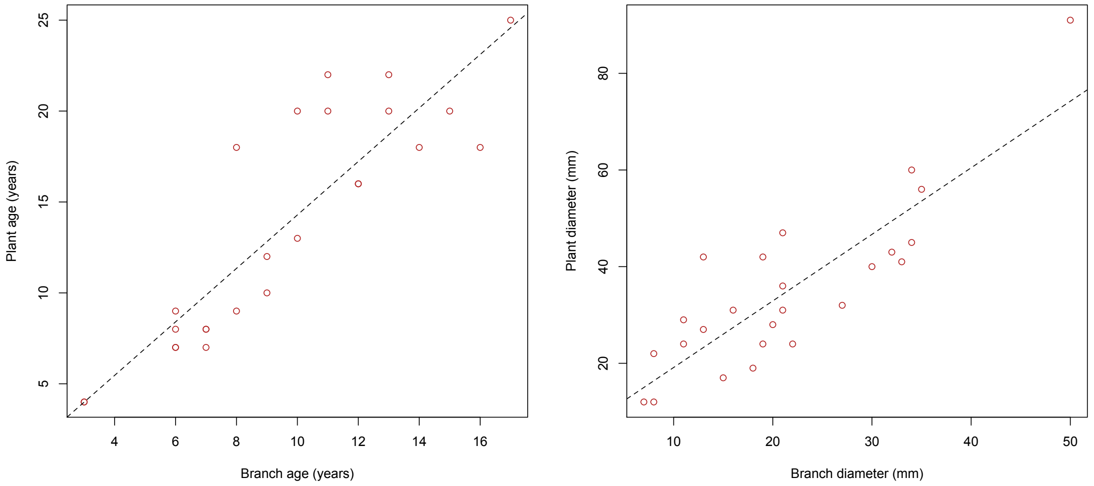

Figure 17. Relationships between branch and plant age and size.

Figure 18. ***M. germanica*** **plant (St. Jakob, Pfitsch, South Tyrol, 20/07/2017).**

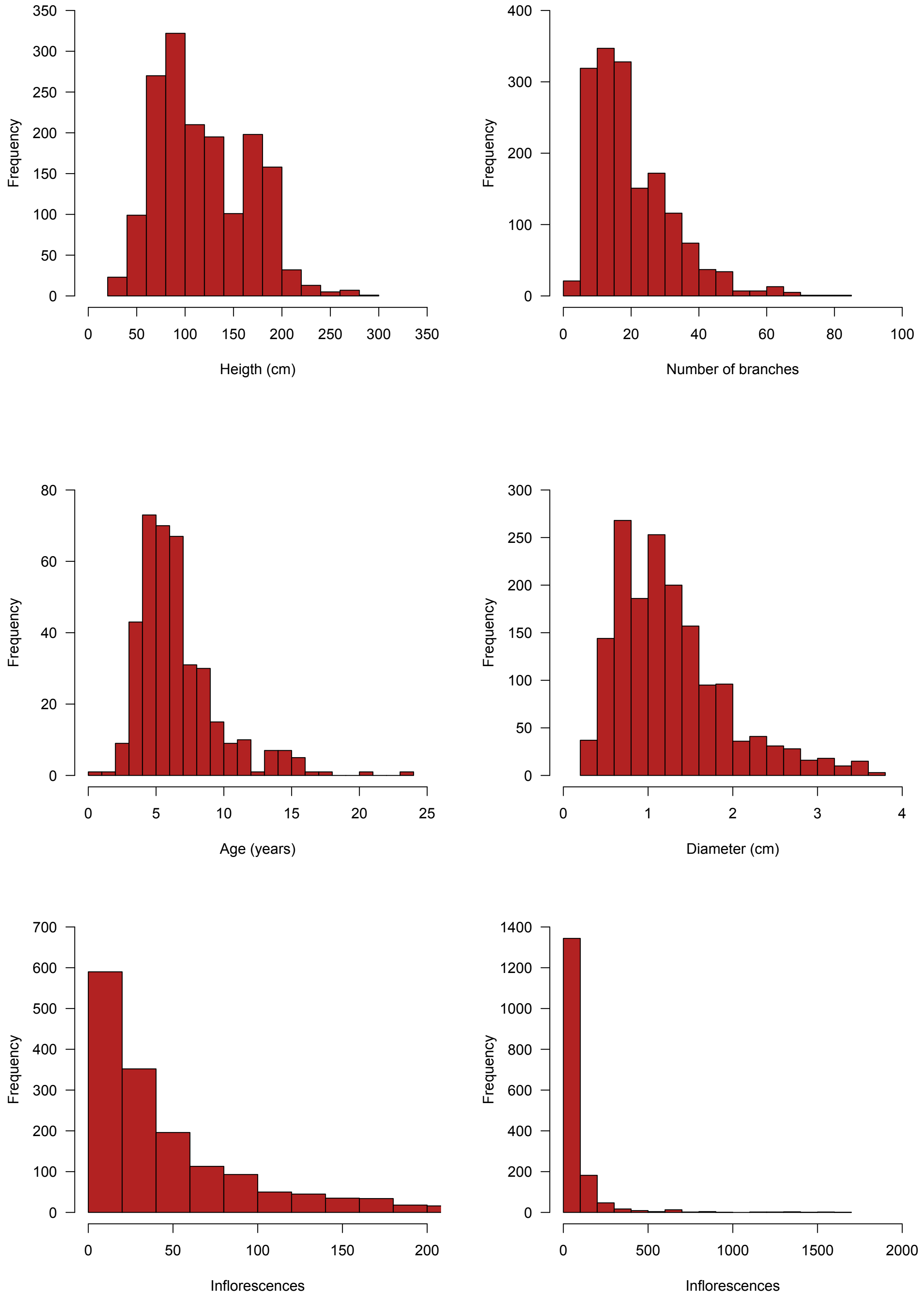

Figure 19. Histograms of the frequencies of the measured traits.

The distribution of height, diameter, age and number of branches is close to symmetric. On the contrary, the number of inflorescences is strongly asymmetric, with many more individuals with < 200 inflorescences (Figure 19). We can conclude that, overall, the populations of north-east Italy (60,000 individuals) are even-aged at the regional scale, with a certain degree of variability among sites. However, the number of inflorescences is a character that is clearly not associated either to individual size or to its age. This must be due to the particular processes that control blooming in this species (Paper I).

The relationship between diameter and height conforms to a linear relationship ($p < 0.0001$):

height [cm] = 48.8 + 58.6 diameter [cm]

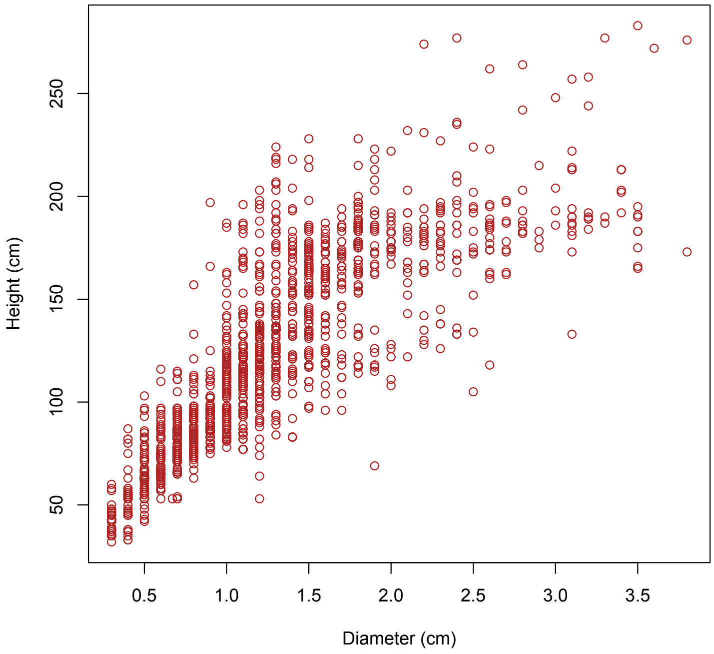

Figure 20. Plot of height against diameter (n = 1,634).

The relationship between trunk diameter at breast height (DBH) and tree height (H) is the most commonly used measurement of tree size. The allometric relationship of DBH and H among individuals at a particular point in time has long been used to describe the strategies of tree species, but this relationship has more rarely been extended to shrub species. Here, the relationship is clearly linear until about 2 cm, beyond this value height growth declines more than diameter growth, which is similar to the pattern observed in trees.

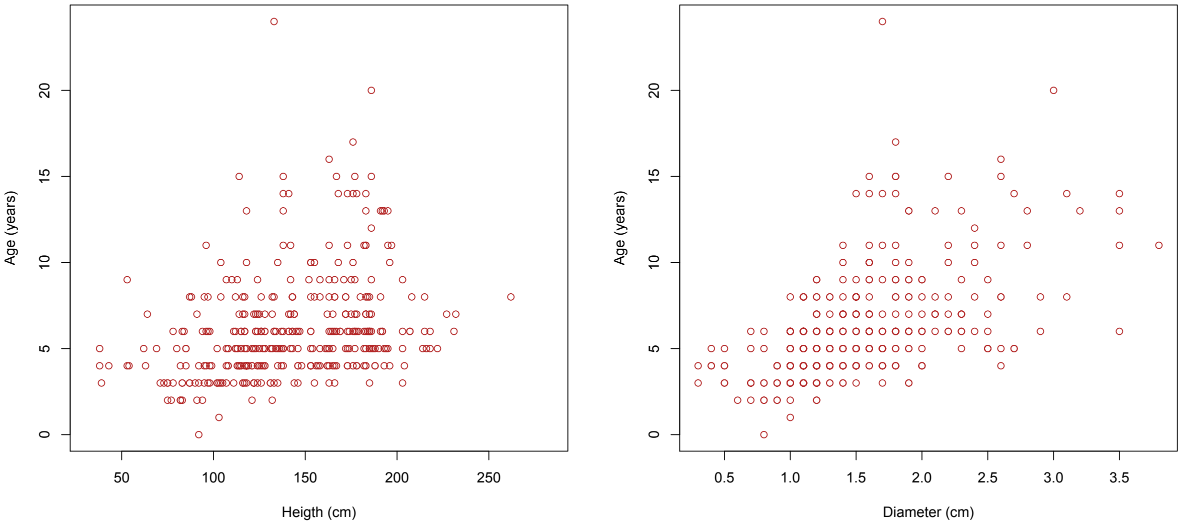

Figure 21. Relationships between age and size (n = 382).

The relationship between age and size (both diameter and height) is also significant ($p < 0.0001$), and conforms to the following functions (Figure 21):

age [years] = 2.34 + 2.50 diameter [cm]

age [years] = 2.38 + 0.026 height [cm].

It is remarkable how, even in a mostly dynamic ecosystem, *M. germanica* confirms the expectation that associates age with size.

4.3. Basin-level

4.3.1. Basin-level description of *M. germanica* sites

The description of the three basins was presented in § 3.2.4. The aim here is to provide some details about the *M. germanica* site conditions, grouped by those three basins: Adige, Piave and Tagliamento.

Adige basin has a much wider gradient of elevations than the other two basins, particularly if compared with the Tagliamento River, where the *M. germanica* individuals are mostly located on the floodplain (Figure 22). The Piave River shows intermediate elevations. As a consequence, we expect that *M. germanica* in the Adige river is subject to river dynamics typical of Alpine rivers.

This is confirmed by the pattern of active channel width, which is negatively correlated to the altitude (Figure 23).

Figure 22. ***M germanica*** **population on Tagliamento River, 275 m a.s.l., at Tolmezzo, Udine Province (07/10/2017).**

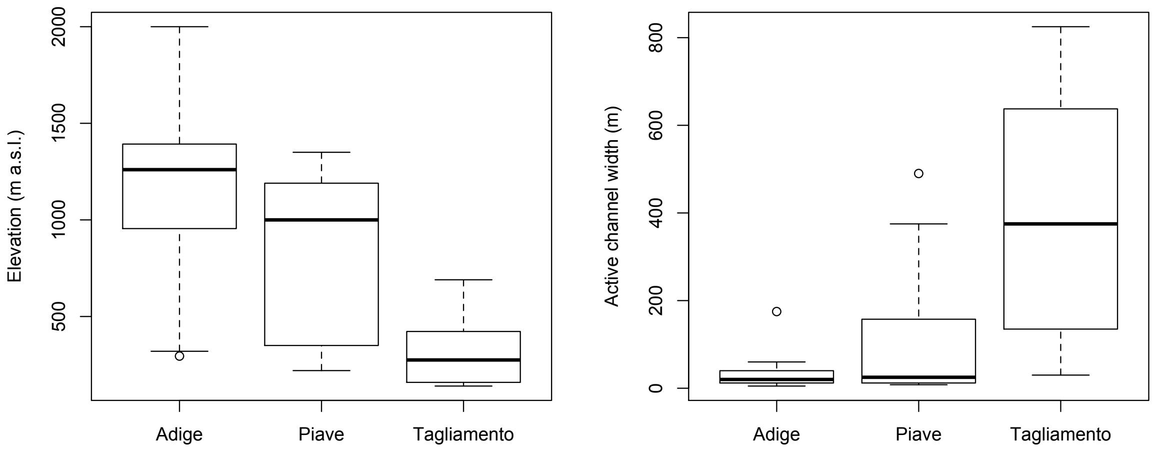

Figure 23. Box-plots showing the elevation and active channel width in the three basins.

Moreover, this is confirmed by the site length that follows the same pattern as the active channel width (Figure 24).

Tagliamento basin has the median highest number of *M. germanica* individuals per site, followed by Piave and Adige basins (Figure 25), the density pattern is the opposite, because of the larger area occupied by the populations (Figure 26). It is also evident that the distribution of *M. germanica* individuals shows outliers, represented by unusually densely populated sites, particularly in the Adige basin.

It is confirmed that there is a significant difference between the three basins in the number of adults per site (p = 0.00132), multiple comparison of means by Tukey contrasts showed that Piave has more adults than Adige, but this difference is only marginally significant (p = 0.10); Tagliamento has significantly more adults than Adige (p = 0.0013), while Tagliamento and Piave did not show any differences. No difference in number of juveniles was detected between the three basins.

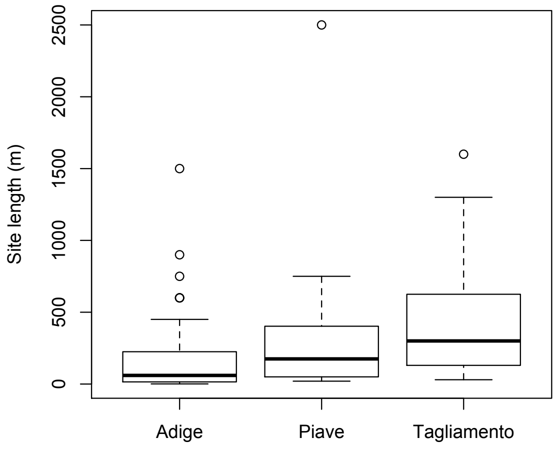

Figure 24. Box-plot showing the *M. germanica* site length in the three basins.

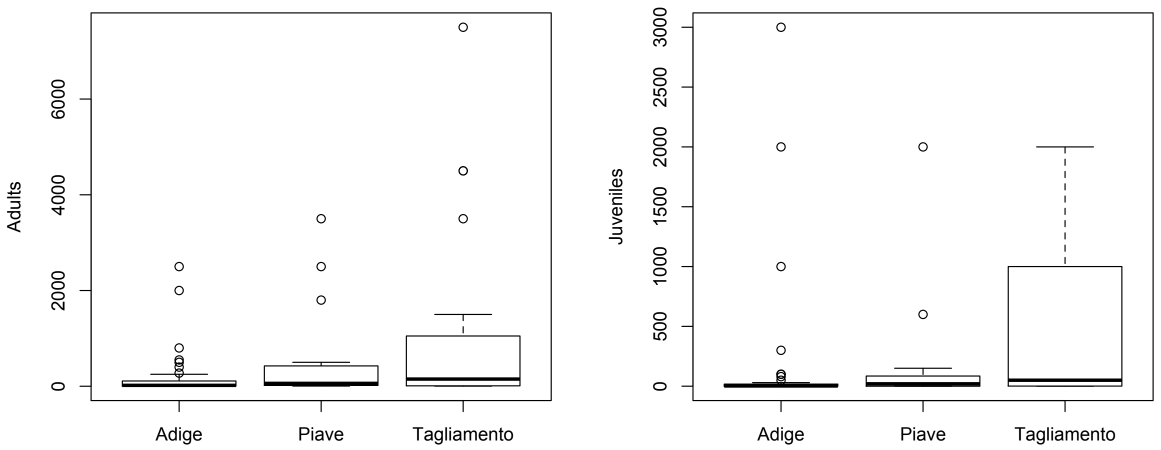

Figure 25. Box-plot showing the *M. germanica* abundance per site in the three basins.

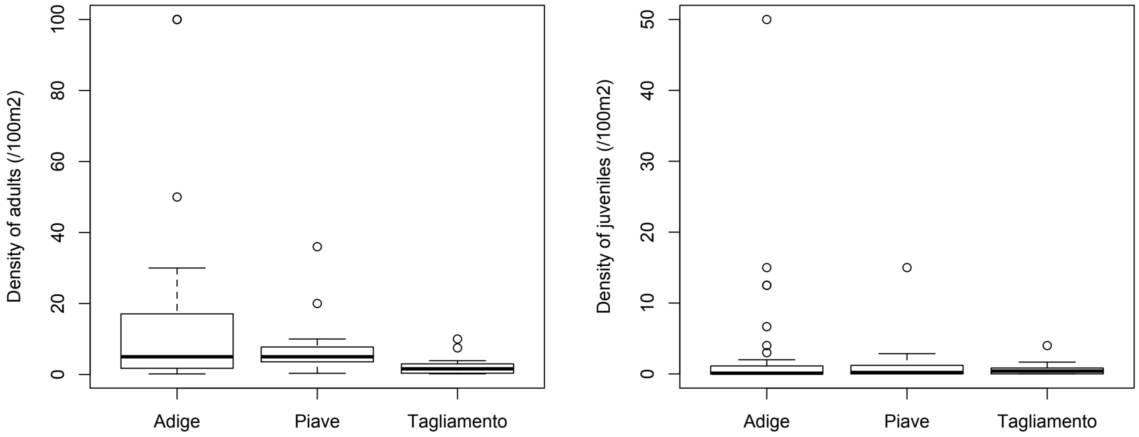

Figure 26. Box-plots showing the *M. germanica* density per site in the three basins.

4.3.2. Relationships between basin identity and *M. germanica* traits

In the Adige basin the plants have a higher average age (7.1) than the Piave (5.4) and Tagliamento basins (4.5). In the Adige basin plants are taller (127.9 cm), with a bigger diameter (1.3 cm), larger numbers of branches (22.4) and inflorescences (108.7) (Table 3).

This seems to be linked to the less dynamic conditions of the more regulated streams in the Trentino-South Tyrol Region that allow the plants to live longer. Moreover, many sites are relict with no regeneration. In the Tagliamento basin, characterized by greater natural dynamics, the life of *M. germanica* plants is shorter and their dimensions are smaller. In the Piave basin the presence of some less viable populations and some young populations probably influenced the traits averages, particularly the lower average number of inflorescences.

Table 3. Mean (µ), median (m) and standard deviation (σ) of *M. germanica* traits in the three basins (n = 1,634).

Basin	Height [cm]			Diameter [cm]			Inflorescences			Branches			Branch age [years]		
	µ	**m**	**σ**	**µ**	**m**	**σ**	**µ**	**m**	**σ**	**µ**	**m**	**σ**	**µ**	**m**	**σ**
Adige	128	122	47.9	1.3	1.2	0.71	109	42	205	22	18	13.9	7.1	6.0	3.3
Piave	110	94	46.5	1.1	1.0	0.54	30	18	32.5	16	14	8.7	5.4	5.0	2.7
Tagliamento	109	103	43.3	1.2	1.1	0.65	54	34	50.8	18	16	8.4	4.5	4.0	1.7
All	118	112	47.2	1.2	1.1	0.66	73	32	149	20	16	11.8	6.1	5.0	3.1

The number of inflorescences are statistically different between the three basins ($p < 0.0001$). Multiple comparison of means by Tukey contrasts confirmed this order of decreasing mean: Adige > Tagliamento > Piave.

4.4. Regional-level

M. germanica spontaneous individuals counted in 2017 in the whole study area ere 59,776, of which 70% were adults (Figure 27).

The relationship between adults and active channel width is positive and marginally significant ($p = 0.078$), while the upstream closeness of a check dam ($p < 0.0001$) is significantly negative. These are the only significant relationships found between the response variables and explanatory variables. This means that the number of juveniles cannot be modelled at the regional scale.

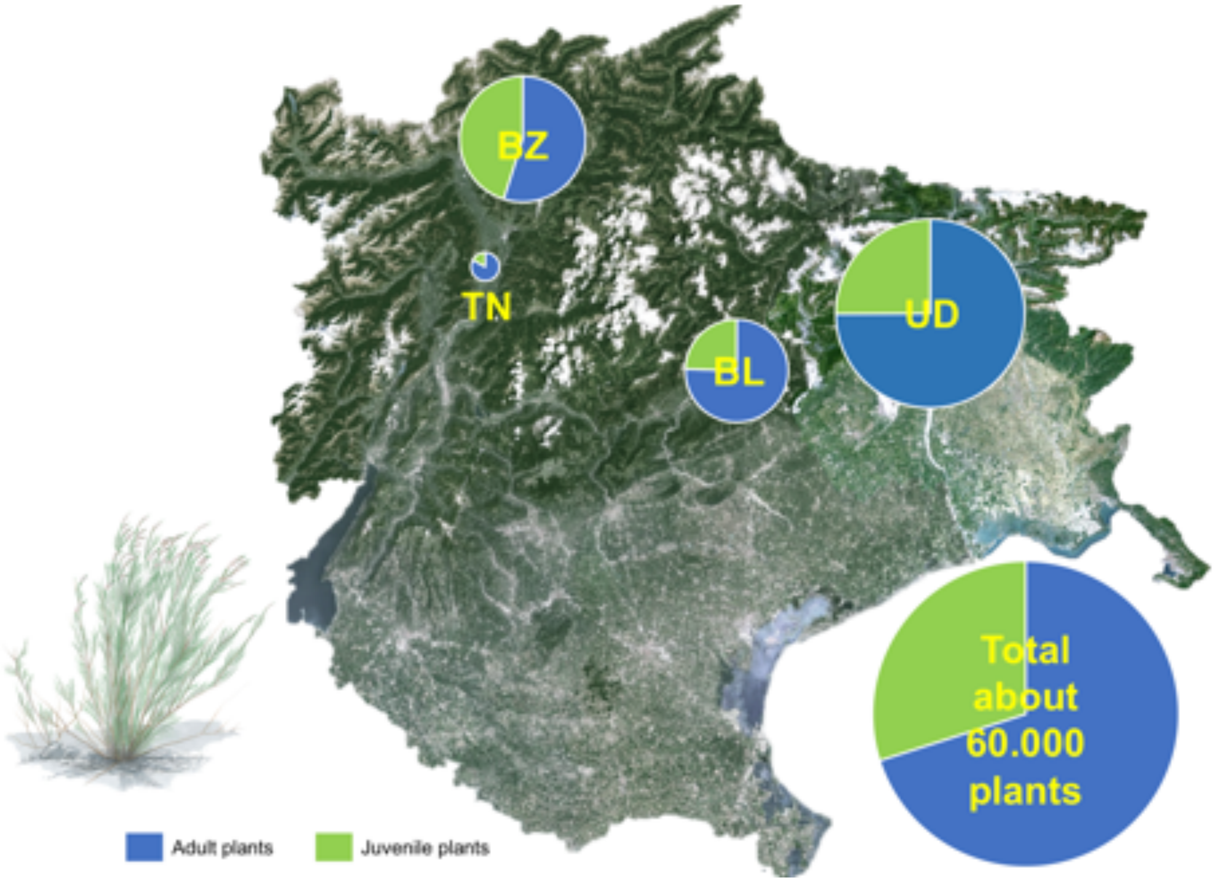

Figure 27. The total number of *M. germanica* individuals counted in north-east Italy, distinguished distinguished between juvenile and adult plants and among provinces (BZ: Bozen, TN: Trento, BL: Belluno, UD: Udine).

5. General conclusion and further research

This thesis investigated: a) the available information on the biology of *M. germanica* growing in Central Europe (Paper I); b) factors that affect the long-term population dynamics and viability of *M. germanica* (Paper II); c) if integrating the time series of population data could change the results of the objective b) (Paper III); d) the determinants of the success of reintroduction projects, given by the post-plantation establishment of viable populations (main text); e) whether a difference in the *M. germanica* traits existed among three rivers having different bio-climate, geology and fluvial morphology affected by different intensities of anthropogenic disturbance (main text); f) the total size of and the factors that affect the population abundance of *M. germanica* at a regional scale (main text). The above points correspond to the thesis objectives.

We collected the available information on the biology of *M. germanica*, **objective a)**, with a review (Paper I) of the description, uses, cultivation, propagation and conservation status. The aim is to publish this review in a journal series that summarizes the available information on individual species. Diethart Matthies, editor-in-charge of the Journal Perspectives in Plant Ecology, Evolution and Systematics has expressed interest for publication in the series "Flora of Central Europe". We therefore hope that the efforts made to collect literature sources from several countries and written in several languages, and that span several centuries will serve to better understand the dynamics of a threatened plant species in Europe, but also to manage its populations in the alien range of New Zealand.

We studied the dynamics of adult and juvenile *M. germanica* at 19 sites over a 10-year period (2009–2018) along a 30 km long stretch of an Italian Eastern Alpine river, by assessing a set of anthropogenic and geomorphological factors (Papers II and III). This research achieved **objectives b)** and **c)**. From 2009 to 2015, adult (239–571 individuals) and juvenile (62–292 individuals) population numbers showed no significant difference between years, and a remarkably uneven distribution among sites. Yet, several remnant populations have declined or disappeared in recent years and a few populations have increased. We found a positive effect of the width of the active channel on adult and juvenile plants. This means that anthropogenic river narrowing is a leading cause of the decline of the species along riverbanks. For juveniles, abundance also decreased with distance from downstream check dams. We conclude that in the regulated river studied, the conservation of *M. germanica* appears to be possible not only as a result of natural flow dynamics, but also at an artificial sediment storage area upstream of a check dam with a semi-natural river dynamic that maintains favorable riverine habitats. Integrating the time series (2009-15) with a further three years (2016-18) we confirmed that active channel width is one of the main determinants of adult abundance, but not of juvenile.

One important observation of such a long time series is that if one year or just two had been surveyed, or even the first and last year, the results would have been different. This confirms the relevance of time series in biodiversity conservation.

The results of the reintroductions (**objective d**) by bare root cuttings planted in Bozen province are positive for a few restoration projects that are more relevant in terms of size. However, the more limited projects did not give positive results. We found that one of the main determinants of success is the active channel width. One important reason for failure is the use of only bare root cuttings and the planting season which should not be close to the spring flooding. In any case, the choice of plantation site, up to the fine spatial scale, should be coherent with the biology and ecology of *M. germanica*. Instead, many of the plantation sites were in zones characterized by strong interspecific competition from willows and alders, or too far from the active channel. We would also like to point out that, thanks to the sharing of data by a public agency, we were able to test the effect of a - de facto - 20-year long experiment. This data sharing should be more common among public agencies and we wish to express our gratitude.

We have demonstrated that some important relationships between morphological and chronological traits exist in *M. germanica*, namely between height, diameter, and age (**objective e**). We were also able to find a function relating plant age and age of the largest branch. We hope that this will help to further deepen our knowledge about the dendrochronology of this shrub species, without the need to uproot single individuals. We noticed a wide variability in the number of inflorescences, which were unexpectedly higher in the most elevated and human-impacted basin (Adige). One explanation is the greater age of individuals and the less frequent floods in the more regulated rivers. However, we stress that the number of inflorescences, as well as the mean age and size, is not necessarily an indicator of the viability of the populations. This is due to the particular biology and ecology of the species (see Paper I).

When all the rivers and basins are taken together (**objective f**), we found only two fundamental relationships. The first confirms what we have already shown for the Avisio River: the correlation between adults and active channel width. We also confirmed that the number of juveniles is less easily associable to the collected environmental variables. One interesting result is the negative influence of an upstream check dam on adult abundance, which is another signal of the value of *M. germanica* as an indicator of wild natural rivers.

At the beginning of this research we wanted to analyze data on soil texture (sediment size frequency) and flood frequency. We assume that both these variables are able to influence the long-term dynamics of *M. germanica* and would therefore be good predictors of adult and juvenile abundance. Moreover, it would be good to integrate the database with information regarding whether the population is living.

The collection of data from the few gauging stations was difficult and, unfortunately the time series is often not complete and far from the *M. germanica* sites. This, and time constraints, prevented us also managing this part of the database. We also collected leaf material from 1,500 individuals distributed over the entire study area. They were dried in tea bags and are currently stored inside zip-lock plastic bags with silica gel to maintain a level of dryness. Our hope is that they will be used for genetic analyses.

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Appendix: Papers I-III

Paper I

Biological Flora of Central Europe: *Myricaria germanica* (L.) Desv.

Bruno Michielon, Tommaso Sitzia

1. Introduction

Myricaria germanica, German tamarisk or False tamarisk, is a typical pioneer shrub on gravelbars in braided alpine rivers in the temperate zone of Europe and Asia. Over the past 150 years this species has suffered a dramatic reduction in Europe as a result of anthropogenic changes in watercourses. This species is therefore a perfect indicator of natural rivers, but its survival is also possible along regulated rivers, the crucial limiting factor being the absence of natural disturbances that might drive primary succession. This review presents the current state of knowledge and related management implications.

Taxonomy

The genus *Myricaria* is not easy to classify, partly because its members show few distinctive external features. There is often a marked polymorphism, and the characters of shoots of different age and length, position and density of racemes can differ but not be reliable for a distinction between two species. Sometimes species recognized in the past are not distinguishable by a complex of morphological characters, grow in the same area and do not exhibit any distinctions in ecological growth conditions.

Some distinct species that were recognized in the past, are currently considered growth form types living along ecological gradients from colder high altitudes to warmer low regions.

Moreover in the 19th century botanists collected plant samples of tamarisk, perhaps of the same species, in many mountain regions of Central Asia and described them for the first time in different regions. The absence of a comprehensive description and exact locality often presented great difficulties to scientists studying *Myricaria* species.

Incompleteness in the description of morphological characteristics also derives from the fact that plants are only studied from herbarium specimens. *Myricaria* taxonomic status is often questionable. In fact, different names indicating different recognized species by botanists in the past, have been reduced in recent years to synonyms of the same species for their similarity and joint growth.

2. Description

The name of the genus derives from the ancient Greek common name for tamarisk plants "μυρίκη", cited in two verses of the Iliad (X, 466; XXI, 18), in the first Idyll of Theocritus and in the Historia Plantarum of Theophrastus (3rd century BC). Matthioli in his Discorsi (1559) refers to the Materia Medica (1st century AD) by Dioscorides who wrote about the medicinal properties of the "mirice" or "tamarigio", supporting the hypothesis that the tamarisks, belonging either to the genus *Tamarix* or *Myricaria*, have been attributed to the same type of shrub.

One of the earliest botanical descriptions of the species is by Gaspar Buhin. In his Pinax Theatri Botanici (1623) the plant is referenced as "Tamarix fruticosa folio crassore: sive Germanica" ("Bushy Tamarix with fleshier leaves or Germanica") that belongs to the group "Myrica" or "Tamariscus". A wider description of the species, reporting its preference for water, was made by his brother Johann and J.H. Cherler (1651). They report a copious presence of the species along central European frequently flooded sandy riverbanks. The species is later described by other pre-Linnaean botanists (Rey, 1673; Toumefort, 1700). Linnaeus described the species *Myricaria germanica* (L.) Desv. as *Tamariscus germanica* in his Species Plantarum (1753) as living in flooded habitats of Central Europe ("Habitat in Germaniæ locis inundatis"). In his book he referred to a painting of the species by Lobelius (1591).

According to the most recent (26.02.2018) checklist in one of the most credited world vascular plant databases (Hassler, 2018), *M. germanica* is a member of the Tamaricaceae family, which contains other 109 species and 5 genera: Hololachne (1 species), Myricaria (15 species), Myrtama (1 species), Reaumuria (22 species), and Tamarix (71 species). The database recognizes 13 synonyms and two subspecies of *M. germanica*: subsp. *germanica* and subsp. *pakistanica*, the latter being first described by Qaiser (1976). In Europe, the only currently accepted taxon of *Myricaria* is *M. germanica*. *M. ernesti-mayeri*, described by Lakušić and Pavlović (1971) as a distinct species in Serbia, Montenegro and Kosovo based on its morphological features, is not currently recognized as a separate taxon from *M. germanica*.

The species belonging to the Tamaricaceae family are shrubs, undershrubs or trees with slender, flexuous branches, rarely herbs, halophytic, rheophytic or xerophytic (Gaskin, 2003). Leaves are usually small, often scale-like, alternate, simple, exstipulate, usually sessile, sometimes sheathing, rarely subsessile, generally fleshy and with punctate salt secreting glands. Flowers are grouped into racemes, panicles, spike-like racemes or spikes, sometimes solitary, actinomorphic, bisexual or rarely unisexual with plants dioecious or hypogenous. The genera *Tamarix* and *Myricaria* are very similar, the only consistent difference being that there are 10 connate stamens in *Myricaria* versus 4 to 14 distinct stamens in *Tamarix*. *Myricaria* tends to have sessile, cushion-like stigmas (or at least no obvious style or style branches) and a stipitate seed pappus, while *Tamarix* tends to have a short stylodium and a sessile pappus, but there are exceptions (Gaskin et al., 2004).

The genus *Myricaria* was established by Desvaux (1825). Niedenzu (1895) provided its first classification. A recent phylogenetic analysis of the Myricaria genus by Zhang et al. (2014) identified 4 clades, Parallelantherae, Renantherae, Alpinae and Laxiflorae, the second of which *M. germanica* belongs to. Currently the genus occurs in Northern Temperate zone of Eurasia, mainly along the Asian mountains, and it is especially common from the Mediterranean basin to Central Asia. The crown age of *Myricaria* is ca. 20 Ma, and diversification of the 4 clades occurred in the Himalayas 8.83-6.35 Ma (Zhang et al., 2014). *M. germanica* followed a dispersal route from the north-west Himalayas, across the Iranian mountains, Caucasus, Crimea and the Carpathians. The Himalayas therefore serve as the center of origin for *Myricaria* where it is endemic and remarkably diversified (Zhang et al., 2014).

2.1 Morphology

Stems and branches

M. germanica (Fig. 1) is an erect shrub that attains maximum heights of 1-3 m in the lower altitudes of the temperate zone and assumes a dwarf trailing form at higher altitudes and in the boreal zone. Stems are numerous, erect to ascending, the old ones with black, rough surface, richly and irregularly branched. Stems are formed by long- and short-shoots. Long-shoots are sympodial, with basic to mesotonous support of the shoot system (Hegi, 1975), erect, straight or slightly flexuous, angular in cross section with young one-year parts yellowish-brown and older parts dark reddish-brown. Outer bark is finally silvery-grey, peeling off in flakes. Short-shoots are about 10 cm long, developing from nodes of the long-shoots (those of the current year as well as those of the previous year), secondarily branched from most or all nodes, thereby appearing plumose (Karlsson, 2010).

Branches are erect and densely leafy. Long-term drives, which come directly from the root neck, belong to the first branch order, from these, long branches of higher branch order, until the 5th, develop yearly. The length growth of the long shoots ends no later than the death of the terminal fruit stands. At this point, however, secondary thickness growth has not yet been completed. Below the main flower stand, the long-wheel drive lignifies and can produce new long-tails next year (Opitz, 1993).

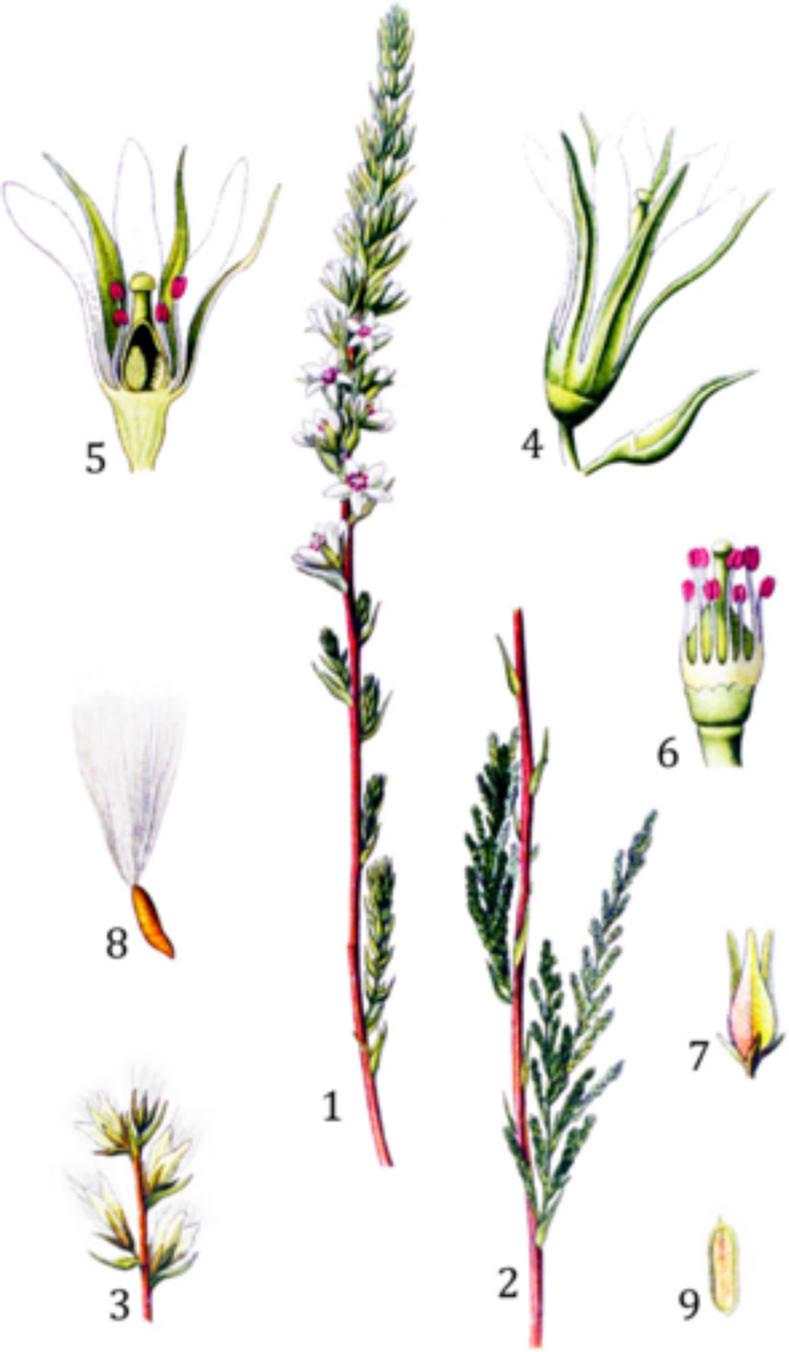

Fig 1. ***M. germanica:*** **1) Flowering shoot: tip of the long shoot with the terminal inflorescence and underlying enrichment shoots; the latter arise from scale-shaped bracts; 2) parts of the flowering plant: the leaves are flat, narrow and alternate; 3) part of the peduncle 4) short stemmed single flower with bract; the 5 lineal, about 3 mm long sepals are membranous at the edge; the 5 petals are pink or white, about 4 mm long; 5) flower in longitudinal section with the narrow pyramidal ovary; 6) flower after removal of calyx and petals: the outer 5 of the 10 stamens are longer than the inner 5; the anthers are purple to red; 7) cracked capsule fruit; 8) seeds with the stalked hair; 9) cut longitudinally-elongated seeds. 4) to 9) enlarged. (from Kurt Stueber, modified from Thomé 1905).**

Leaves

Leaves are simple, alternate and sessile, without stipules, thick, greyish-green, punctate from salt-excreting glands, small, larger on the main than lateral branches (Gaskin, 2003; Hegi, 1975; Karlsson, 2010). In contrast to the linear, flattened cotyledons, all subsequent leaves are greatly reduced in size (Dörken et al., 2017). Leaves of distant long shoots, borne on prominent, persistent cushions, are 5–11(–13.5) mm long, narrowly triangular to linear-lanceolate, acute or slightly obtuse; leaves of closely set short shoots, are 2.4–5(–7) mm long, narrowly lanceolate to narrowly elliptic, obtuse (Karlsson, 2010).

One of the most particular and historically noted (Vuillemin, 1887) peculiarities of this plant are the glands and secretions, weakly developed in young leaves, but in mature leaves, particularly those on distal parts of the shoot axis, attain a high density on the abaxial side of the leaves (Fig. 2). The secreting surfaces of the sunken glands are surrounded by crown-like epidermal cells, with a total diameter of 60-90 µm. The morphology indicates the presence of orthorhombic crystals containing $CaSO_4$ and granular clusters of fusiform crystals of Mg-containing $CaCO_3$. These "salt glands" said to be a characteristic feature of the family of Tamaricaeae can function principally as an adaptation to secrete Ca in a highly calcareous soil in a habitat where NaCl is ecologically unimportant (Dörken et al., 2017).

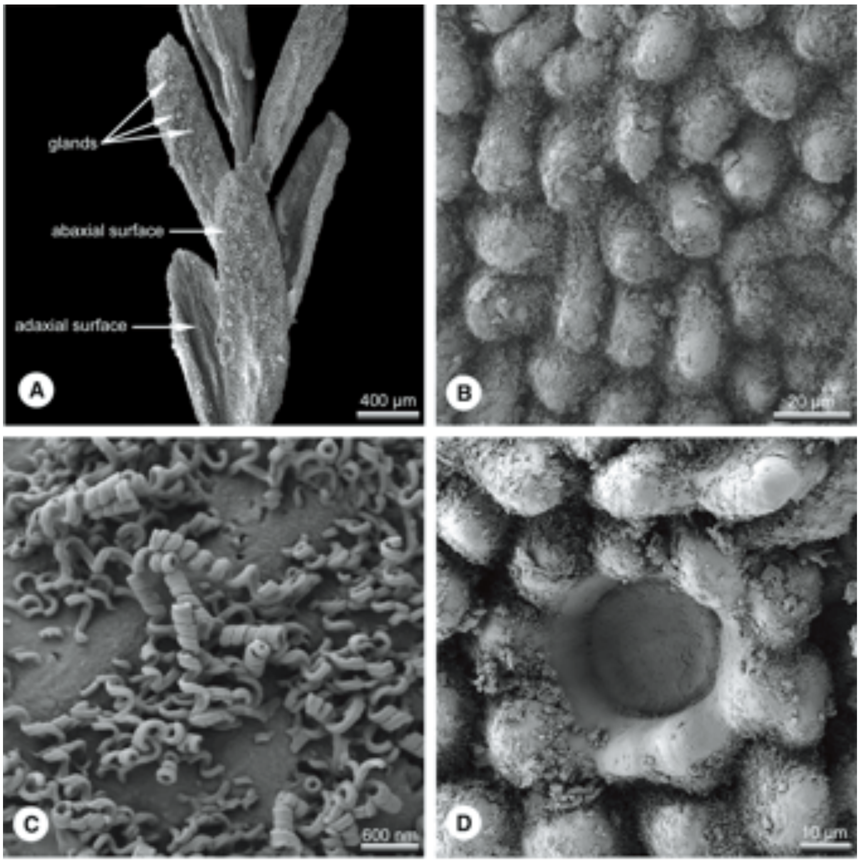

Fig. 2. *M. germanica*, details of mature leaves: a) leaves at the distal part of a shoot axis; abaxial surface with several secretions; adaxial surface without secretions; b) papillae-shaped epidermal cells; c) cuticular waxes strongly curled; d) gland without secretion, the secreting surface is surrounded by crown-like cells (from Dörken et al., 2017).

In *M. germanica*, all leaves, except the cotyledons, are orientated with their adaxial side towards the shoot axis. To reduce water loss via the lamina in these leaves, the epidermal cells on the light-exposed side become thicker and are about double the size of those on the shaded side. This functional transformation is exclusively caused by solar radiation, depending on which part of the leaf is shaded and which is light-exposed. The stomata are only developed on the shaded surface (Dörken et al., 2017).

Flowers

M. germanica is a monecious and synoecious shrub. Flowers are aggregated in simple or compound racemes, which are terminal on long shoots of the current year and on elongated lateral shoots on the long shoots of the previous year, dense, spike-like, in flower 3-6 x 1.1-1.5 cm, in fruit 5.5-23 x 1.7-2.8 cm, with 20-70(-100) flowers; middle pedicels 1.4-3.6 mm (Gaskin, 2003; Hegi, 1975; Karlsson, 2010). Flowers are actinomorphic, pentamerous (occasionally tetramerous) and small. Sepals are (3.2-)3.6-5.8(-6.8) mm long, narrowly lanceolate, acute, with a narrow scarious border, sometimes strongly red-tinged at the base. Petals are white-pink, narrowly oblanceolate to broadly linear, obtuse, 4-4.9(-5.9) x 1.5-1.8(-2) mm, slightly shorter to slightly longer than the sepals, persistent in fruit. Disc is absent, ovary is superior, trigonous (rarely tetragonous), slightly contracted toward the apex. Stigma is cushion-like, sessile, in trefoil head (Gaskin, 2003; Hegi, 1975; Karlsson, 2010). Stamens are 10 unequal, monadelphous, filaments connated to the middle, the antesepalous ones being considerably longer, (2.1-)2.9-3.8 mm, than the antepetalous. Anthers are 2-locular, globose, dorsifixed, 0.4-0.7 mm long, obtuse opening by longitudinal slits (Gaskin, 2003; Hegi, 1975). The pollen grains are small (10-25 μm), spheroidal and three-celled (Fig. 3) (Gaskin, 2003; Halbritter and Berger, 2018).

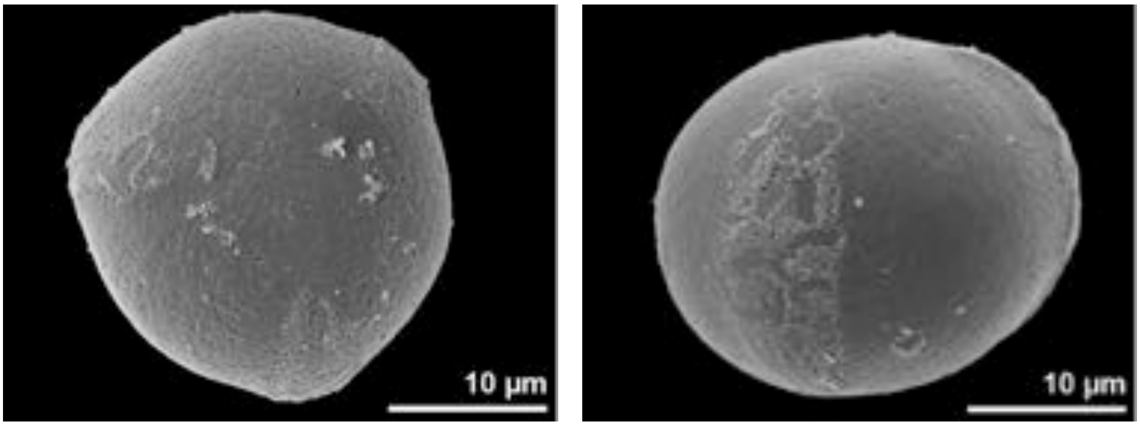

Fig. 3. Pollen of *M. germanica* (a: polar view, b: equatorial view) (from Halbritter and Berger, 2018).

Fruits

After flowering, the upper fruit nodes, which are fused together with three leaves, develop into non-fleshy, dehiscent, loculicidal capsules, narrowly pyramidal, greyish blue with grey-green top, 9-12.5 mm, opening with 3 (-4) valves (Karlsson, 2010). There are more than 100 seeds (Opitz, 1993; Petutschnig, 1994). The capsules open in dryness (Opitz, 1993).

Seeds

The numerous and small seeds are highly evolved and best suited for wind dispersal, having a long stipe that acts as a shaft. Seeds are 0.8-1.5 x 0.3-0.4 mm (Karlsson, 2010) and weigh 007 m.g (Bill, 2000). They are obovoid, irregular-cylindrical, flattened, yellow-brownish, with an apical tuft of long, simple, unicellular hairs that are united at the base. Their surface is fine reticulate and lustreless (Bojnanský and Fargašová, 2007; Karlsson, 2010). Endosperm is scanty or starchy (Gaskin, 2003). They are equipped with 4.0-6.0 mm pappus, which act as an umbrella flyer (Hegi, 1975).

Roots

The excavation of roots in the field is not easy due to the gravelly habitat where the species grows. On individuals collected by the authors along the Avisio River and Cordevole River the vertical development attains more than 1.5 m and lateral more than 2.5 m, depending on the plant groundwater connection.

Wood

M. germanica xylem and phloem have a quite uniform anatomical structure (Fig. 4). The ring boundaries are defined by ring-porosity or semi-ring-porosity. Earlywood vessels attain diameters >100 μm and cell wall thickness of 4-6 μm, which make the annual ring very easy to detect. The relatively small rays of *M. germanica* distinguish it from all *Tamarix* species (Schweingruber et al., 2011).

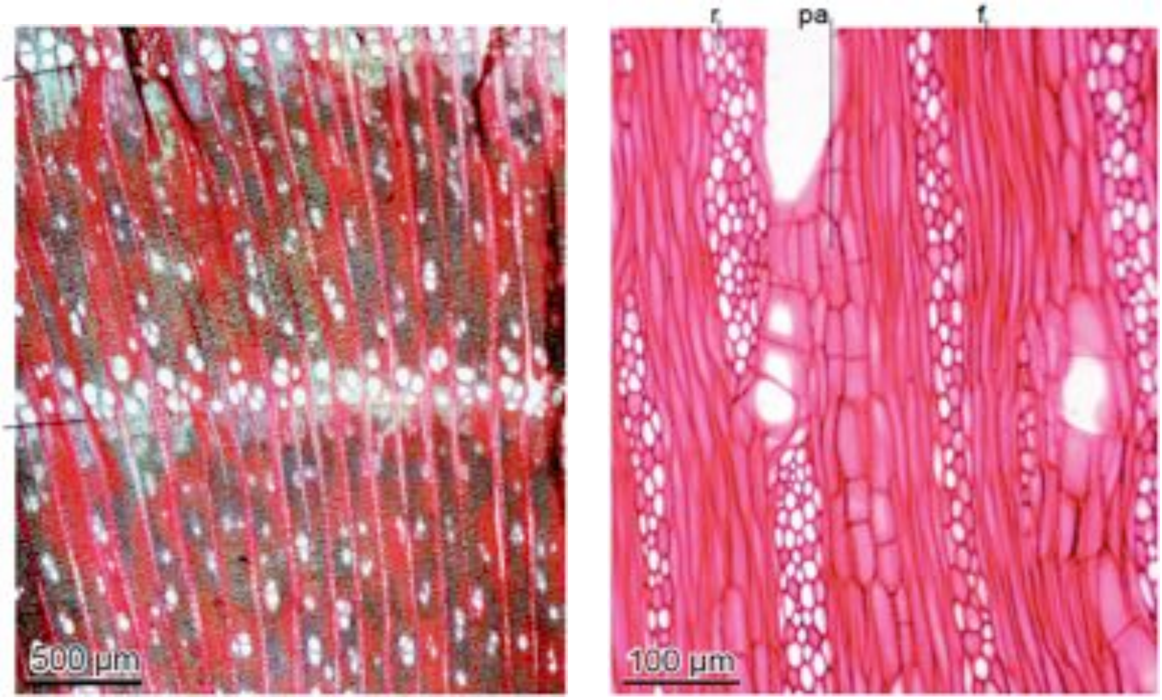

Fig. 4. Transverse section of *M. germanica* in which the ring boundaries are defined by ring-porosity of the wood (on the left). Vessels are solitary or in small, often radial groups. Rays with 4-6 cells in width, partially with sheet cells (on the right). Abbreviations: f: fiber, pa: parenchyma, r: ray. From a stem of a 1.2 m-tall shrub, along a riverbed at the Morteratsch Glacier forefield, Switzerland, 1900-2100 m a.s.l. (from Schweingruber et al., 2011).

2.2. Distribution and habitat requirements

Geographical and altitudinal distribution

The species is regarded as a glacial relict (Hegi, 1975). It is widely distributed in Eurasia (Fig. 6), its native range extending from Mongolia in the east to Scandinavia in the north and the Iberian System in the southwest (Hegi, 1975; Meusel et al., 1978).

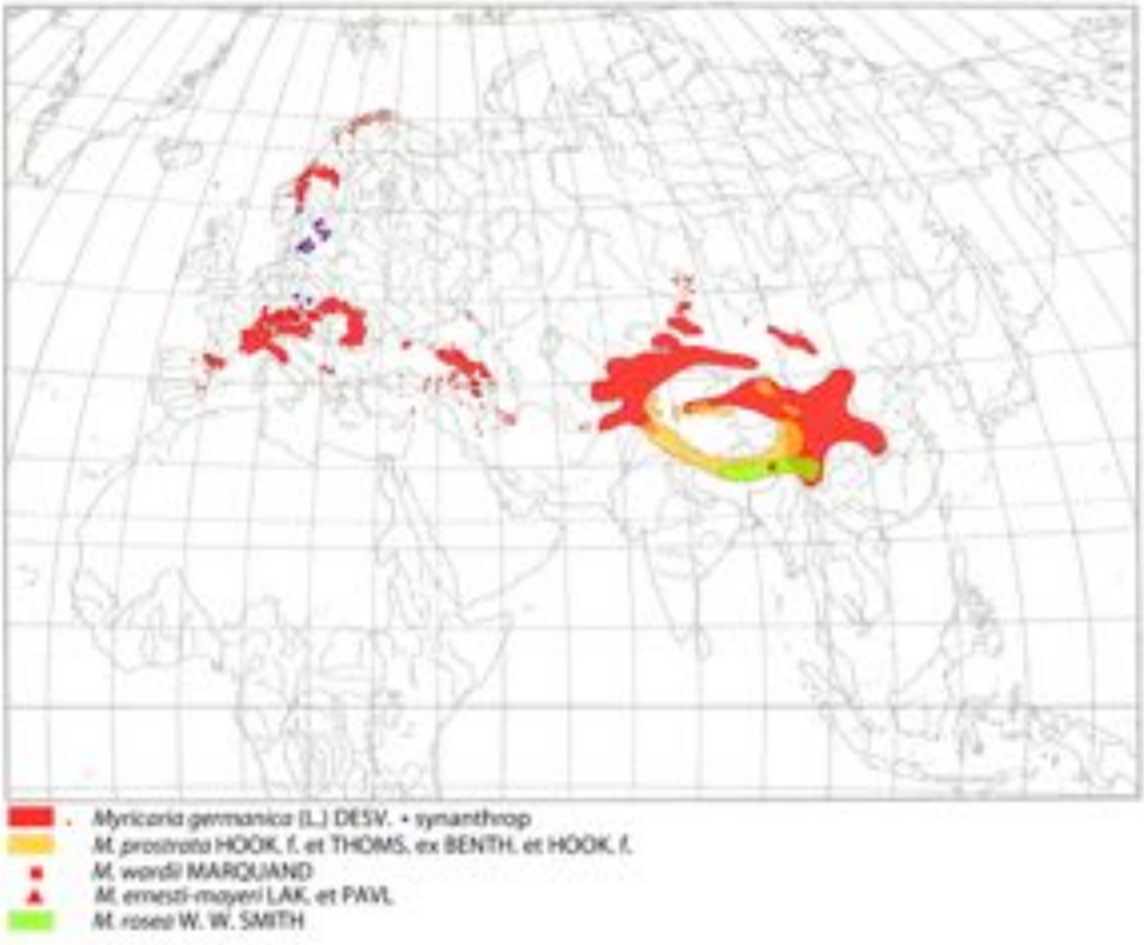

Fig. 6. World distribution map of *M. germanica* (from Lener 2011, modified from Meusel et al., 1978).

In New Zealand *M. germanica* is an alien invasive species of natural braided rivers, first recorded in 1986, on the Canterbury Plains and other eastern areas of the South Island (Heenan et al., 1998; Sykes and Williams, 1999; Williams and Wiser, 2004). *M. germanica* is successful because its ecological niche in New Zealand is wider than in Europe where many competitors are present in the active floodplain zone. The New Zealand *M. germanica* populations are genetically more similar to populations from France, from where it must be undeliberately introduced (Müller et al., 2017).

The theoretical altitudinal range of *M. germanica* includes running waters from high altitudes such as glacier forelands down to sea level.

In Europe, the species mainly comes from the plateau over the montane to subalpine high plateau. In general, the species is widespread in the subalpine environment, but is also present along rivers on the alluvial plains (Hegi, 1975). The highest known occurrence in Europe is in Switzerland on the Valais glacier moraines (Findelen Gletscher) at 2350 m (Hegi, 1975). In France the species reaches up to 1600 m, in Norway the 630 m, in the Bavarian Alps 1100 m, in the Engadin and Graubünden up to 2000 m, in Tyrol 2300 m (Hegi, 1975), in Romania 1656 m (Vinţan, 2016), in South Tyrol, Italy 1865 m (Michielon and Sitzia, 2014). The lowest sites in the south-eastern Alpine region, in Italy, have been located on the high Veneto plain at 50 m along the Brenta River near Cittadella (Masin and Scortegagna, 2011) and on the Friulan hills at about 100 m (Lippert et al., 1995).

Habitat

M. germanica is a habitat specialist, light-demanding pioneer species depending on unstable, open, habitats with a high proportion of fine sand, sufficient water supply for seed germination and low to moderate river dynamics (Karlsson, 2010; Kudrnovsky, 2013a; Müller, 1998; Werth et al., 2014).

It is an explicitly light demanding species, which is unable to grow on shady sites and in willow stands can only be found at their edges (Bill et al., 1997). Its strategy is to thrive in harsh riparian habitat conditions, instead of competing with other species for favorable environments (Kudrnovsky and Höbinger, 2015).

Its narrow ecological niche lies between the "ability to survive" in highly dynamic sites marked by substratum structures and the massive competition suffered by this pioneer species when it is overgrown by shading willows and alders (Wittmann and Rücker, 2006).

According to the classification by Grime (1979), *M. germanica* is a "stress tolerator" and a "stress-strategist", adapted to a lack of nutrition and temporary water shortage, which is driven out by competition (Müller, 1995).

Its traits are highly suitable for colonizing and growing on river gravel or sand bars, provided that they are temporarily and periodically flooded (Prach, 1994). The main habitat limitations are due to the inability of the species to compensate for the high relocation frequency of their locations by appropriate colonization of new areas, and this suggests that their survival strategy is geared more to persistence of once-occupied sites, than to the permanent occupation of new land (Bill et al., 1999). More rarely it colonizes secondary sites such as landslides and debris flows (Michielon and Sitzia, 2014), moraine deposits at glaciers, solifluction slopes, lake shores and pebbly sea-shores (Karlsson, 2010; Petutschnig, 1994), road embankments, dams and gravel-pits (Karlsson, 2010), and industrial wasteland (Rostanski and Wozniak, 2000). It is rarely grown for ornament but may escape from gardens in a few localities where it might be regarded as an alien species, like in Denmark and Southern Sweden (Hultén and Fries, 1986). According to the authors' observation, soil types are mostly sandy or gravelly, alkaline, characterized by low of nitrate and phosphate delivery, even though the species tolerates acidity and a high organic matter content, showing a wide adaptability to different soils.

Since the earliest work of Ellenberg (1974), indicator values referring to the ecology and biology of the species have been proposed by several authors for several Central European countries (Tab. 1). The values reflect the species physiological growth limits and competitive abilities quite well. There are no great differences between one source and another.

Tab. 1. Indicator values for several European regions and countries (number between parenthesis is the highest value in the scale used).

Region or country	Light	Temperature	Continentality	Cryo-climate	Atmospheric humidity	Soli humidity	Variability of damping	Soil reaction	Soil texture	Soil aeration	Nutrients availability	Salt concentration	Carbonate content	Organic matter content	Source
Central Europe	8 (9)	4 (9)	7 (9)	-	-	8 (12)	-	8 (9)	-	-	3 (9)	0 (3)	-	-	(Ellenberg et al., 1991)
Central Europe	8 (9)	4 (9)	8 (9)	-	-	8 (12)	-	8 (9)	-	-	3 (9)	0 (3)	-	-	(Berg et al., 2017)
Czech Republic	9 (9)	5 (9)	-	-	-	8 (12)	-	8 (9)	-	-	3 (9)	0 (3)	-	-	(Chytrý et al., 2018)
France	8 (9)	3 (9)	7 (9)	-	8 (9)	6 (9)	-	8 (9)	5 (9)	-	3 (9)	1 (9)	-	1 (9)	(Julve, 2017)
Hungary	8 (9)	4 (9)	7 (9)	-	-	8 (12)	-	8 (9)	-	-	2 (9)	0 (3)	-	-	(Borhidi, 1995)
Italy	8 (12)	- (9)	7 (9)	-	-	8 (12)	-	8 (9)	5 (9)	-	0 (9)	0 (3)	-	-	(Pignatti et al., 2005)
Poland	5 (5)	3.5 (5)	3 (5)	-	-	4 (6)	-	5 (6)	-	-	3 (5)	0 (3)	-	-	(Zarzycki et al., 2002)
Switzerland	4 (5)	3 (5)	4 (5)	-	-	3.5 (5)	3 (5)	4 (5)	-	5 (5)	2 (5)	- (2)	-	-	(Landolt et al., 2010)
Ukraine	8 (9)	8 (17)	11 (23)	8 (15)	14 (23)	13.5 (23)	10 (11)	9.5 (15)	5 (9)	4 (15)	3.5 (11)	5.5 (19)	9 (13)	-	(Didukh, 2011)

Plant community description

The phytosociological indicator value of *M. germanica* poses some problems. It can be found within different phytosociological orders and associations. According to the syntaxonomical framework proposed by Mucina et al. (2016), *M. germanica* occurs as a young plant in the *Epilobion fleischeri* alliance (class *Thlaspietea rotundifolii*) and as a pioneer plant on river alluviums of the *Salicion eleagno-daphnoidis* alliance (class *Salicetea purpureae*). The associations belonging to the *Epilobion fleisheri* of which *M. germanica* is one of the characteristic species are *Epilobietum fleischeri* Frey 1922, *Myricario-Chondrilletum* Br.-Bl. in Volk 1939 and *Epilobio-Myricarietum germanicae* Aichinger 1933 (Grabherr and Mucina, 1993). In Mediterranean Europe, *M. germanica* is also a characteristic species of the *Andryaletum ragusinae* Rivas Br.-Bl. et O. Bolòs 1958 (Rivas-Martínez et al., 2011). The *Salici purpureae-Myricarietum germanicae* Moor 1958 is the only association belonging to the *Salicion eleagno-daphnoidis* of which *M. germanica* is a characteristic species.

Across its European range, accompanying species pools vary considerable (Essl, 2013), the common species associated with *M. germanica* within all the different communities are: *Achnatherum calamagrostis*, *Agrostis gigantea*, *Anthyllis vulneraria* subsp. *alpestris*, *Calamagrostis epigejos*, *Calamagrostis pseudophragmites*, *Campanula cochleariifolia*, *Campanula cochleariifolia*, *Chlorocrepis staticifolia*, *Dryas octopetula*, *Epilobium fleischeri*, *Epilobium dodonaei*, *Equisetum palustre*, *Erigeron acris* subsp. *angulosus*, *Erucastrum nasturtiifolium*, *Festuca arundinacea*, *Gypsophila repens*, *Hieracium piloselloides*, *Hippophae rhamnoides*, *Juncus alpinoarticulatus*, *Juncus articulatus*, *Juncus bufonius*, *Linaria alpina*, *Phragmites australis*, *Poa alpina*, *Poa nemoralis*, *Chondrilla chondrilloides*, *Populus nigra*, *Salix daphnoides*, *Salix eleagnos*, *Salix nigricans*, *Salix purpurea* ssp. *gracilis*, *Salix triandra*, *Sesleria albicans*, *Thymus praecox* and *Typha minima* (Grabherr and Mucina, 1993).

Kudrnovsky (2013a) distinguishes three main groups and 12 subgroups within the *Salici purpureae-Myricarietum germanicae* in the Eastern Alps, this confirms the wide variability of this association. Moreover, in a recent study, Kudrnovsky and Kalníková (2015) have described nine groups of indicator plant species which represent variations of the *Salici-Myricarietum* vegetation structure according to different site conditions, as follows:

- from lowland to higher altitudes: *Salix eleagnos*, *Salix purpurea*, *Alnus incana*, *Agrostis stolonifera* agg., etc.;
- lowland floodplains: *Salix alba*, *Populus nigra*, *Epilobium dodonei*, etc.;
- floodplains in medium and higher altitudes: *Poa alpina*, *Anthyllis vulneraria* agg., *Epilobium fleischeri*, *Saxifraga aizoides*, etc.;

- fresh and moist conditions: *Deschampsia cespitosa*, *Saxifraga aizoides*, *Carex flacca*, *Carex flava*, *Juncus articulatus*, etc.;
- alkaline fens: *Tofielda calyculata*, *Poa farinosa*, *Poa palustris*, etc.;
- lime rich floodplains: *Sesleria caerulea*, *Dryas octopetala*, etc.;
- pioneer sites: *Tussilago farfara*, *Chlorocrepis staticifolia*, *Epilobium dodonei*, *Campanula cochleariifolia*, *Gypsophila repens*, etc.;
- alkaline floodplains: *Aster alpinus*, *Oxytropis campestris*, etc.;
- more stabilized conditions: *Larix decidua*, *Alnus incana*, *Picea abies*, *Pinus sylvestris*, etc..

M. germanica is also a characteristic species of the European Union habitats 3210 "Fennoscandian natural rivers", 3220 "Alpine rivers and the herbaceous vegetation along their banks", 3230 "Alpine rivers and their ligneous vegetation with *Myricaria germanica*" and 3250 "Constantly flowing Mediterranean rivers with *Glaucium flavum*" (European Commission, 2013).

Paleobotany

The only evolutionary information specifically available for *M. germanica*, which are not generalized to all members of the Tamaricaceae family, concern the leaves. It is known that, due to ecological and evolutionary forces, *M. germanica* leaves reduced their size and increased deciduousness. Moreover, evolution of salt glands was in response to high soil NaCl levels and later enabled colonization of calcium rich soils. Among the Tamaricaceae members, *M. germanica* secretes large amounts of Ca and Mg, probably as $CaSO_4$ and as Mg-containing $CaCO_3$, rather than NaCl; this may have facilitated its adaptation to non-saline Ca-rich soils (Dörken et al., 2017).

2.3 Life cycle, phenology and growth

Leafing, flowering and fruiting phenology

The initial stage is the most critical in the life cycle of this plant (Lener, 2011). The length growth of the long shoots ends no later than the death of the terminal fruit stands. At this time, however, secondary thickness growth has not yet been completed. Below the main flower stand, the long-wheel drive lignifies and can produce new long-tines next year (Opitz, 1993). *M. germanica* produces a remarkable amount of infructescences, and the number of seeds rises exponentially with plant size (Lener, 2011). The inflorescences bloom from the bottom upwards, the bottom buds open first (Petutschnig, 1994). The fruiting and flowering season lasts from May-June to August-September, but variations are possible according to the site altitude and water supply over the growing season (Bachmann, 1997; Kudrnovsky, 2002).

Normal initial maturity age for *M. germanica* is 2-3 years (Bill et al., 1997; Lener et al., 2013). This is influenced by the period of more or less early germination and by more or less favorable environmental conditions. Personal observation is that not vigorous plants can flower for the first time even later, up to 4-5 years.

Longevity

Due to the river dynamics and also the overgrowth by taller-growing species, individuals are generally not older than 20-30 years (Kudrnovsky and Höbinger, 2015), most frequently about 10-15 years (Ellenberg, 1996; Kudrnovsky, 2002). Schweingruber et al. (2007) measured an average age of 7.7 years at the Morteratsch glacier foreland, at 1900-2100 m a.s.l..

The maximum age of plants is subject to local and temporal variability. The death of individuals or at least the death of plant parts is probably genetically determined (Schweingruber et al., 2007), but the maximum age limits are changed and modified by local conditions.

The oldest recently collected tamarisks were 21 years old (Lener, 2011; Schweingruber et al., 2007) or 26 and 22 years old (Lener et al., 2013), but an older record reports 67 well-developed annual rings in a 9.5 cm thick stem, having a rotten core, with an estimated total age of at least 70 years (Frisendahl, 1921). The difference between the maximum and average age is due to the natural flow dynamics, which constantly changes the location of the tamarisk and sometimes also against their growth requirements (Kudrnovsky, 2005). Over time, the tamarisk shrubs often form communities with willows. In the last decades many river beds have been excavated with the consequent lowering of the ground water by a few meters and the original riparian habitat, without river dynamics, has become a dry habitat in which *M. germanica* can survive longer. Recruitment is impossible, but the reduced competition of other shrub-tree species allows *M. germanica* to survive longer than expected (Ellenberg, 1974). In fact, a few 40-year-old plants have been observed growing at Prad Biotope, a site that became arid, along Solda River, at Prad am Stilfser Joch, South Tyrol, Italy (Fig. 7).

Figure 7. Cross-section sections of *M. germanica* plants from South Tyrol of 22, 22, 22, 40 years (from left to right).

Pollination and flowers fate

Pollination is performed by insects in favorable weather, and self-pollination is possible in the case of rain (Hegi, 1975). *M. germanica* is an insect-pollinated, hermaphroditic plant, capable of selfing (Werth and Scheidegger, 2014) like other species of the genus *Myricaria* (Liu et al., 2006), but details of the mating system are not known. The pollen grains of *M. germanica* show high germination (Opitz, 1993) with up to 96.0% fertility (Jeelani et al., 2011).

Embriology

M. germanica, as a member of the Tamaricaceae family, has several important embryology features: two-celled pollen grains, nucellar parietal cells, several types of tetrasporic (*Fritillaria*, *Adoxa*, *Chrysanthemum cineraraefolium*, *Drusa* and *Plumbagella*) embryo sac, nuclear endosperm without haustoria, Solanad type of embryogeny with a massive suspensor, frequent occurrence of polyembryony, exalbuminous, exarillate, simple exotestal seed, and seed-coat derived from the outer integument only (Johri et al., 1992). Studies on *M. germanica* have highlighted the coexistence in the same plant of an unusual variety of types of development of the female gametophyte, always built according to the tetramegasporial scheme (Battaglia, 1941, 1943, 1988; Dahlgren, 1927; Frisendahl, 1912; Gates, 1924; Maheshwari, 1937; Traub, 1939; Zabban, 1935).

Fruit production

The upper fruit, which are fused together with three leaves, develop into grayish, often reddish, pyramidal, septic capsules, that open in dryness (Kammerer, 2003; Opitz, 1993). More than 100 tiny seeds develop in these 12-mm-long and top-pointed fruit capsules (Opitz 1993, Petutschnig 1994, Bachmann 1997). The number of seeds in fruit non-parasitized by insect larvae is on average 129 (87-189), while in parasitized fruits it is 126 (65-189) (Lener, 2011).

Calculating the number of seeds produced per plant per year is very difficult, since the species forms new flower and fruit stands as well as new fruit nodes during the whole summer (Lener et al., 2013). Therefore, maximum diaspores production and the current one can therefore only serve as a point of reference (Bill 2000).

In general, the flowering and fruit set strongly depend on the size of the tamarisk and vary from a minimum of 2 to a maximum of 2758 flower and fruit stands per plant. Tamarisks older than 4 years are able to develop many flower and fruit stalks, but the number of inflorescences is still very variable: a number from 2758 to 325 inflorescences were counted on different mature plants at the end of May. A 3-4 years old shrub had 661 inflorescences, 2-3 years old tamarisks had only 2 to 18 flower or fruit stalks (Lener et al., 2013). Bill (2000) reports from 12,000 to 150,000 (maximum value of 200,000) diaspores per individual. Like flowering and fruit set, seed production also increases exponentially with the size of the tamarisks. For example, Lener (2011) reports a maximum seed production, over the summer, from about 9,000 seeds in a 2-3 years old plant, to 12,700,000 seeds (estimated 125.97 seeds/fruit) for a big shrub older than 4 years, with 2758 flowers and a maximum production of 100,695 fruits (estimated 36.51 fruits/flower). At the end of July, Lener et al. (2013) report a production by a 2-3 years old plant of an average of 22,000 seeds (4,000-38,000), by a 3-4 years old an average of 480,000 seeds (80,000-1,390,000) and by plants older than 4 years an average of 3,306,000 seeds (700,000-5,800,000). This calculation was done assuming that a fruit stand has an average of 66 ovaries, 17 of which are mature capsules that currently release their seeds.

Seed dispersal

Seed lightness makes them predestined for a long-range dispersal by wind (Lanz and Stecher, 2009), but dispersal through water is also possible (Bill et al., 1997).

Propagation by wind can take place upstream or downstream (Werth and Scheidegger, 2014) until distances that are not exactly proportional to wind speed. The majority of seeds fall next to the plants, but distances of up to 25 m have been recorded at a wind speed of 1.9 km/h (Lanz and Stecher, 2009). Fink et al., (2017) reported an average threshold of 30 m from the source of propagules, Bill et al. (1997) a distance of more than 100 m, using water-filled trays (Stöcklin and Bäumler, 1996) and, occasionally, a dispersal distance of several kilometers is possible (Bill, 2000). For example, a recent natural site (Fruscalzo, 2012) has been found 10 km away from the nearest population.

Dispersal kernels derived from seed trapping experiments confirms that establishment of a *Myricaria germanica* metapopulation is not limited by habitat availability but by the proximity of potential habitats to source populations (Harzer et al., 2018).

Between 3,300 and 3,500 seeds per m^2 have been found close to the tamarisks, but 400-600 seeds/m^2 can still be found at 90 m (Lener et al., 2013). The seed rain of the *M. germanica* population is extraordinary high (Müller and Scharm, 2001) and Lener (2011) measured a maximum seed pressure of about 500,000 seeds/m^2 (17/07/2010).

Diaspores can also float, so they can be dispersed by water (Bill et al., 1997). Seeds are able to reach new suitable habitats thanks the "water" transport (Bill et al., 1997; Lanz and Stecher, 2009). It is possible that seeds can be transported over long distances by water, despite the rather short floatability and reduced germination rate.

Bill et al. (1999) assessed that seeds of *M. germanica* can float for about 6 hours, and suggested that a distance of more than 200 km is possible in the water at a flow rate of about 30 km/h. Lanz and Stecher (2009) found in their experiments that seeds that were not exposed to turbulence could float on the water surface for more than 10 days, and that the pappus is well attached to the seed and does not break down even with strong and prolonged turbulence. Werth et al. (2011) demonstrated a clonal propagation over 15 km using molecular genetic methods and propagation of the same species by seed over 8 km. The pappus therefore has an important role in seed buoyancy (Lanz and Stecher, 2009). However, long-range seed dispersal by water is subject to limitations due to natural and man-made barriers (canyons, dams) along river networks (Werth et al. 2014). In any case, germination experiments showed that seeds germinate very well in the water with the restrictions described above, which confirms that they are capable of reaching suitable new habitats via water transport (Bill et al., 1997; Lanz and Stecher, 2009).

Germination

Seed germination is the limiting factor for species persistence. *M. germanica* has the capability to germinate immediately, within four hours, without dormancy, under favorable conditions, after contact with wet sediment (Müller and Scharm, 2001), but germination ability within a really short time and is limited after 48 h (Bill et al., 1997), due to their limited nutrient and storage tissue (Lanz and Stecher, 2009). The colonization potential differs strongly in the typical habitats with *Myricaria* depending on the water regime (glacial, nival and pluvial) and geology of the rivers (Kudrnovsky and Kalníková, 2015).

The dispersed seeds must therefore reach a suitable location as soon as possible in order to germinate. The germination process is made up of several steps: first the radicle breaks through the seed coat; as the hypocotyl stretches, the seed coat is discarded, the hypocotyl extends, the cotyledons become green; the greening can also happen when the brownish thin and therefore translucent seed coat is not yet thrown off. The hair is an outgrowth of the seed coat that remains with it (personal observation).

The seeds are sensitive to light and moisture, especially dew (Hegi, 1975; Lener, 2011). Germination is slowed down by yellow light, while it is positively influenced by pale violet light. Only slightly moist seeds can germinate in the dark (Hegi, 1975). For successful establishment, the interplay between frequency of rearrangement, nature of the substrate and associated water supply and light conditions are of great importance (Opitz, 1993; Bill et al., 1997; Kammerer, 2003; Schweingruber et al., 2007). This requires locations that are outside the normal range of the outflow, water level fluctuations should be very low (Kammerer, 2003). In this first phase, from germination to the formation of deep roots, such favorable conditions are rare (Petutschnig, 1994). The colonization density by *M. germanica* seedlings is therefore also very low in their typical habitat, such as gravel and gravel banks with flooding, dry periods and rubble overburden (Bill, 2000).

M. germanica can germinate rapidly in water with > 90% after only a few hours, a presumably important adaptation in such a dynamic living space (Bill et al., 1997; Lener, 2011). This is also associated to the short storage duration, so that, after 50 hours, over 70% of seeds are fully developed (Lener et al., 2013). In a germination test Lanz and Stecher (2009) found a germination rate of 76% for seeds that were 24 hours old. The plant's capability to germinate can even be expanded, if the seeds are kept in a refrigerator. *M. germanica* benefits from moist conditions, and pre-germinated seeds can be dispersed to new sites via water. Seeds kept in the refrigerator for different periods of time (2 to 41 days) showed almost identical germination dynamics, the seeds germinating within a few hours. After 50 hours, more than 80% of seeds had already germinated. The germination rates did not change with the increase in storage time and reached similar results as the experiments with fresh seeds. Germination rates of ≥ 94% were observed and ≥ 88% of all seeds developed fully, thus completely breaking free from the seed coat (Lener et al., 2013). The river water temperatures are also clearly below the air temperature in summer and correspond approximately to the storage temperatures in a refrigerator within the framework of germination experiments. The good germination rates of cooled seeds suggest that seeds transported in river water remain vital over a longer period of time (Lener, 2011).

In contrast, high temperatures during germination can lead to seedling death. In some cases the radiculata still broke out, but had a yellow and not green color (Lener 2011), meaning they were dead or decaying.

Seedling and adult growth

While the seeds germinate very quickly, slow growth during the first vegetation period has been observed (Kammerer, 2003). In this first phase, from germination to the formation of deep roots, favorable conditions are rare (Petutschnig 1994), so the population density of *M. germanica* seedlings in their typical habitat (gravel and gravel banks with flooding, dry periods) is very low (Bill, 2000), but occasionally in wet sand it can reach over 100 seedlings/m^2 (personal observation). The subsequent development of the plants is very slow (Bill, 2000; Wittmann and Rücker, 2006).

On the whole, the short-term germination, fast-growing germination and slow growth in the first year are a reason for the low establishment success of *M. germanica* (Bill, 2000), and responsible for the competition weakness of this species against *Salix* spp. and *Alnus incana* (Bill et al., 1997; Wittmann and Rücker, 2006).

A fast germinating process followed by very slow growth combined with a strong resistance to water stress seems to be vital in the habitat of *M. germanica*. The slow growth after the germination process could be due to an enhanced investment in root development. This would explain the good resistance to water stress. Seedlings of *M. germanica* are notably resistant to water stress and are only severely affected if the stress lasts several weeks once the plants have reached secondary leaves. This resistance might depend on the population and ancestor they come from (Benkler and Bregy, 2010).

As a conclusion, in the first phase of germination to the development of deep roots *M. germanica* can therefore only establish under favorable conditions that are not present every year (Petutschnig, 1994). Once established, under controlled conditions, sapling growth is 0.15 cm/day in the first 40 days of life. Already at that young stage, average root length (3-7 cm) is longer than the above-ground sprouts (0.9-3.4 cm), at one year old, the sprout length is between 3.8 and 23.2 cm (Lener, 2011).

In plants older than 4 years the mean length of long shoots that bear a flower or fruit base is 231 cm and the mean length of the fertile section is 94 cm (Lener, 2011).

Roots growth

The growth rate of the primary roots is rather low, although the seedling invests a lot of energy in the first few months to develop a proper root system. The delayed growth rate of the primary root is probably the main reason why most seedlings are not able to establish, and as a consequence the rate is very low. Young plants show a strong, strongly wooded primary root (Lener, 2011).

Above all, it is questionable to what extent already extended primary roots are still able to intrude into the substrate and give the young plants sufficient biomechanical stability.

Even if the excavation of the plants in the field proved to be difficult, it was hardly possible to completely open the roots. For one year old plants Lener (2011) measured an average longest root of 33.60 (26.5-39.2) cm and an average above ground sprout of 6.68 (3.8-9.7) cm; the longest root was 39.2 cm (the shortest 18.0 cm). Assuming a linear function for the relationship between root growth and seedling age, there is an average increase in length of 0.11 cm per day (Lener, 2011).

These root lengths can give the plants a groundwater connection that allow them to survive on superficially drying out soils (Bill et al., 1997). An increase in primary root diameter of over 1 cm per year was measured for a 4-year-old plant. (Lener et al., 2013).

Vegetative regeneration

In addition to seed dispersal by water and wind (Bill et al., 1997; Lanz and Stecher, 2009), there is also vegetative propagation through resprouts from roots and stem parts (Staffler, 1999). The ability of vegetative regeneration and excellent regeneration after mechanical damage is the most important adaptation of *M. germanica*, which enables it to survive on dynamic, flooded gravel and gravel banks (Bill et al., 1997; Egger et al., 2010). Branches that are bent down can also become rooted and newly expelled, since tamarisks have the capacity to lower the lower limbs in some circumstances (Opitz, 1993). Thus, long shoots lying in the water and covered by the substrate can form roots. Whether these then become separated from the mother plant is not known (Opitz, 1993).

2.4 Population dynamics

Long-term information on the population dynamics of *M. germanica*, and factors affecting its population density and viability, is limited to a study performed on a regulated river, where abundance of individuals has been monitored for several years (Sitzia et al., 2016). Population numbers showed no significant difference between years, and a remarkably uneven distribution among sites. Population sites did not fluctuate simultaneously and showed different persistence dynamics. This means that if one population becomes extinct the same fate is not likely to occur for the others (Liebhold et al., 2004), with important implications for ecological restoration. A positive effect of the width of the active channel is evident on adult plants, while it is only marginally significant for juveniles (Fig. 8). For juveniles, abundance also decreased with distance from downstream check dams. This means that in the regulated river studied, the conservation of *M. germanica* appears to be possible not only as a result of natural flow dynamics, but also at an artificial sediment storage area upstream of a check dam with semi-natural river dynamics that maintains favorable riverine habitats (Sitzia et al., 2016).

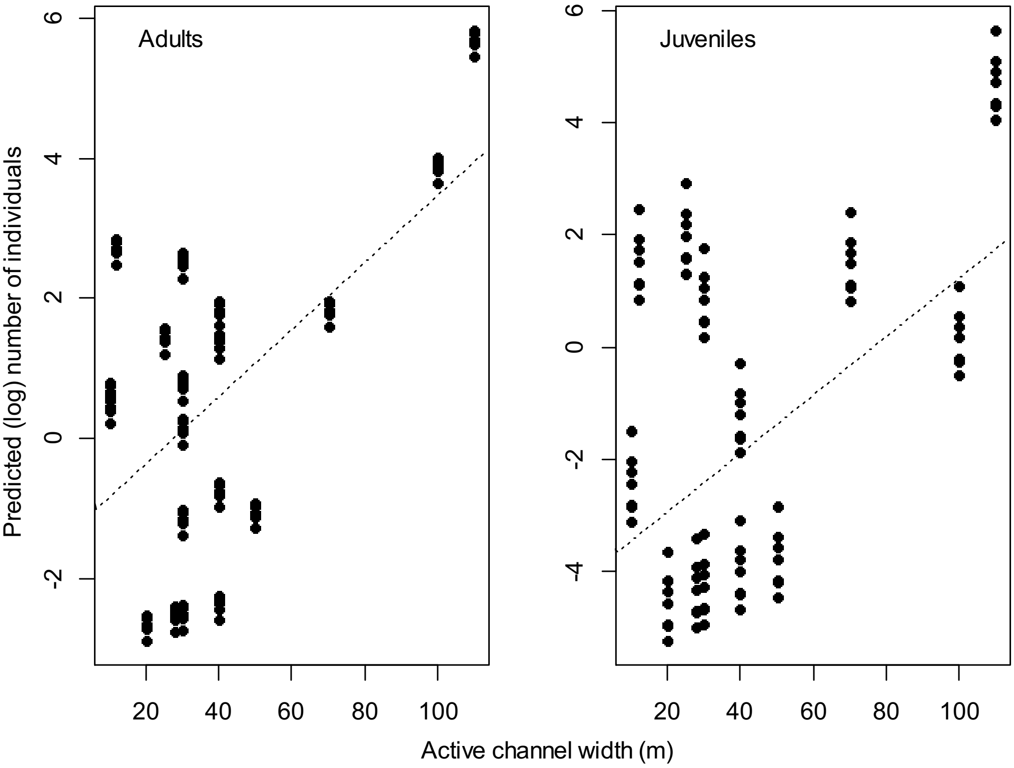

Fig. 8. The effect of active channel width on adult and juvenile *M. germanica* plants (log values) at 19 sites over a seven year period (2009–2015) along a 30 km stretch of the Avisio River, Fassa Valley and Fiemme Valley, Trentino, Italy. The predicted values presented here were calculated from a generalized linear mixed model (Sitzia et al., 2016).

2.5 Response to abiotic factors

Climatically, *M. germanica* is best suited to continental and mountain zones. The frequency and intensity of floods and droughts that characterize the habitat are the most important disturbances to which the species reacts. The limiting factor for seedling survival is a sufficient supply of water. When the groundwater surface beneath the gravel sinks tamarisks suffer from water deficiency and slowly die. Lowering of the groundwater has a greater effect than a lack of precipitation during the vegetation period (Opitz, 1993). However, in dry conditions, more root biomass is produced, preferentially fine rather than structural roots, with the aim of developing the rhizosphere and maximizing water collection; this is combined to a reduction of the aboveground biomass, thus reducing evaporation (Lavaine et al., 2015). This is coupled with the ability to store water in leaves (Kammerer, 2003). It is possible that *M. germanica* resists vessel cavitation, which is an important trait for drought tolerance and has been observed on the close species *M. laxiflora* (Tao et al., 2010).

M. germanica is dependent on fluvial dynamic sites, which are always freed from disturbing competitors, although lacking special adaptations to resist flooding at the physiological level (Kerber et al., 2007).

Long term studies of aerial photos and recently done population studies at the diverted reach of the Isar River (Reich et al., 2008, Harzer et al., 2018), high lighten the importance of extraordinary floods (of the century) for population dynamics of *M. germanica* in diverted river stretches.

Injured and gravel covered plants can sprout repetitively within a few weeks (Bill et al., 1997). Bent-down branches can also re-root and cross through a layer of gravel and sand, up to 20-25 cm thick, sprouting again after only two weeks (Bill et al., 1997), even long shoots lying in the water and covered by the substrate can form roots (Opitz, 1993). *M. germanica* is firmly anchored in the substrate with its far-reaching roots and can also colonize coarse-grained sites in groundwater connection. It is classifiable as moderately flooding-sensitive.

Flooding of the *M. germanica* rhizosphere induced slight decreases in net photosynthesis at an external partial pressure of CO_2 of 35 Pa within the first 10 days. 35 days after flooding it reached only 55% of the level of unflooded control plants. There was no recovery of gas exchange after flood termination. Vitality, rejuvenation and density of individuals of *M. germanica* are significantly lowered in these areas. Therefore, although the plant dominates in a natural location only at flood-affected sites, the gas exchange of *M. germanica* is sensitive to a flooding of the root space under laboratory conditions. Flood duration at natural site should never exceed more than seven days (Kerber et al., 2007).

2.6 Response to biotic factors

Competition by plants

M. germanica is shade intolerant, which is why it is outcompeted by species growing in more stable environments, like willows and alders (Bill et al., 1997). Because the species is weak in competition there is a strong need for recurring disturbances for establishment. The significance of submersion and therefore of flood events is not only the recruitment of new individuals, but also that almost all competitors of *M. germanica* do not survive this or their abundances are at least kept low (Bill et al., 1997).

In general, *M. germanica* does not develop dense vegetation canopies (Kudrnovsky, 2015). The average density of plants is around 5/100 m^2, the maximum known size of a population is 8,500 with local density of a maximum 100 juveniles (10 adults)/m^2 and 100% canopy cover (Sitzia et al., 2016). In such conditions, intraspecific competition may cause a decrease in the proportion of individuals.

Herbivory

Herbivory by mammals is known for the snow leopard (*Panthera uncia*), where entire droppings have been composed by tamarisk and up to 41% contained twigs 2-4 cm long

(Mallon, 1991). The leopards have seen feeding deliberately on the plants, particularly during the mating season (Chundawat and Rawat, 1994). Potential, but tentative explanations for this behavior are roughage, digestion, anti-parasite and supplemental diet (Sunquist and Sunquist, 2002). Wild ungulates and livestock have also been occasionally observed feeding on twigs.

Several insects and mites (e.g., Curculionidae, Eriophyidae, Gelechiidae, Itonididae, Momphidae, Psyllidae, and Tortricidae) are host specific to Tamaricaceae, sometimes cause galling and bud teratisms (Kovalev, 1995). The insects that are closely related to *M. germanica* are: *Coniatus tamarisci* (Fornasari, 1997), *C. repandus* (Fornasari, 2004), *Merulempista cingillella* (Robineau, 2011), *Istrianis myricariella* (Huertas-Dionisio, 2012), and *Diorhabda elongata deserticola* (DeLoach et al., 2003). The dipter *Egle concomitans* Pandelle, 1900 is a probable depositor of eggs that develop into larvae who feed on seeds (Opitz, 1993), like *E. myricariae* Grossmann, 1998.

Seed predation

Parasitizing of seeds by insect larvae, probably belonging to the fly *Lasiomma concomitans* (Pandelle, 1900) has been reported in about 10% of capsule fruits, leading to a maximum loss of about 50% of the seeds (from 126 to 65/capsule) (Opitz, 1993).

Fungi, viruses, mycorrhiza and symbionts

More than 50 fungal taxa may be unique to Tamarix species, among these there are approximately 5-10 unique fungal species for each Tamarix species (Thambugala et al., 2017). Although specific data for *M. germanica* are not available, a close species, M. laxiflora, hosts 26 genera of endophytic fungi classified into 5 subphyla, 7 classes, 12 orders, 17 families (Tian et al., 2015) and present dark septate fungal associations (Zhao et al., 2016). Arbuscular mycorrhizal fungi (AMF) are one of the most widespread types of symbiotic associations, but very few studies have been conducted in riparian transitional zones between aquatic and terrestrial ecosystems (Zhao et al., 2016), including *M. germanica*, which, to date, lack any investigation, but we expect that they could be present to resist stressed environments.

2.7 Physiology

The diurnal variation of photosynthesis records a maximum at noon, with higher values in a wider valley, where prolonged sun exposure causes both water and gravel to become warmer.

The seasonal dynamics of photosynthesis in the climatic conditions presents low values until the beginning of May-June because of the reduced foliar surface and low content of chlorophyll pigments and maximum values in the months of July and August, with a peak in the flowering period. The chlorophyll amount in leaves is reduced, the highest content being recorded in May-June, when leaves reach maturity, and is not influenced by the humidity of the substrate. The transpiration seasonal variation shows maximum values in May-June, due to a large amount of water in the medium and also because of the fact that young leaves lose higher amounts of water through their thin cuticle (Buse-Dragomir and Niculescu, 2017).

2.8 Biochemical data

Most plants of the genus *Myricaria* were found to contain phenolic compounds, including *M. germanica*, which hosts 24 compounds, of which flavonoids are the majority and most active (La, 2011; Swilam, 2014). Three of these isolated compounds have not previously been reported to occur in nature. In the leaf cuticular waxes 4 different series of alkanediols were identified (Jetter, 2000). No other investigations on *M. germanica* are known.

2.9 Genetic data

The genus *Myricaria* has 24 chromosomes (Frisendahl, 1912). Somatic (2C) nuclear DNA content (number of DNA base-pairs) in a zygotic cell is 2,872 Mbp. The amount of DNA (number of DNA base-pairs) contained in one set of chromosomes is 1,436.18 Mbp. Percentage of guanine and cytosine (GC) bases in nuclear DNA is 40.8% (Šmarda et al., 2018)

The genetic structure of *M. germanica* populations has been analyzed using microsatellite markers. 22 nuSSR microsatellite loci on the nucleus and 5 cpSSR loci on chloroplast have been used by Werth and Scheidegger (2014). Gene flow between neighboring populations was found both upstream and downstream. Some dispersal events might be associated to human-induced dispersal, such as during conservation reintroductions. In isolated populations, like most European ones, there is a substantial population subdivision, which was expected and can be explained not only by isolation by distance, but also by the frequent selfing. This creates a strong population structure and permits it to be concludes that *M. germanica* has a metapopulation structure, with the majority of gene flow occurring among neighboring populations. Dams and canyons can disrupt the gene flow, which should be reactivated through restoration of channelized rivers (Werth et al., 2014). Peripheral populations can be subject to a low diversity due to their position, geographically isolated from other populations by large mountain ranges and because high summer drought hinders the survival of new seedlings each year, leading to genetic drift (Werth et al., 2014). These general rules might not always be confirmed, indicating stochasticity by long-distance dispersal and extreme flooding events (Werth and Scheidegger, 2014). The barcode of the species can be retrieved from the freely available data security model BOLD (Ratnasingham and Hebert, 2007).

3. Uses

Medicinal uses

In ancient medicine *M. germanica* was applied for various treatments, especially for spleen diseases. For example, a decoction of young twigs was used by the Tartars in cases of rheumatism and bruises (Loudon, 1838). Edmund Grindall, who brought it from Germany after he was made Archbishop of Canterbury cultivated it chiefly for its medicinal virtues. and Master Richard Hakluyt, in 1599, tells us that "many people have received great health by this plant" (Loudon 1838). In Europe, the importance of *M. germanica* as a possible medicinal plant has been forgotten (Madaus, 1938), even if the green compressed leaves and boiled roots of *M. germanica* were used as medicine and tamarisk oil was used for inhalation and embrocating (Kiem, 1992) and its balsamic bitter bark as an astringent (Lindley, 1846). A decoction of the bark is aperient and was used in Spain in the treatment of jaundice (Chopra and Nayar, 1956).

In many Asian countries (more commonly in China, Mongolia and India) the genus *Myricaria* is still used for the treatment of some infections, certain types of intoxication, liver diseases, scalds, joint pains, sore throat and arthritis (Gewali, 2011; Kirbag et al., 2009; Kletter et al., 2008; Lyakh and Tsybulya, 2009; Semenova, 1993; Singh, 2012).

Tibetan medicine uses it for treating central neurogenic pains with the advantages of a strong analgesic effect (Baima et al., 2011). *M. germanica* is used for the treatment of rheumatism, including acute and chronic rheumatoid arthritis, impervious measles, organs toxic heat, sore throat, poisoning, yellow fever, blood embolism fever (Li et al., 2005). Aerosol is used for treating acute/chronic sprain, contusion, lumbar muscle strain, trauma, pain, hyperosteogeny, stiff neck, periarthritis humeroscapularis, rheumatosis and rheumatoid disease, with the advantages of advanced formulation, simple process and quick action (Li and Liu, 2009). A Tibetan cream, toning lotion and emulsion containing *M. germanica* is known to have a moisturizing effect, and can improve and prevent skin roughness (Yamamoto et al., 2007). Mixed with other species, medicated toothpastes are prepared for hemostatic, anti-inflammatory, analgesic and repercussive effect, oral cavity cleaning and care (Lei et al., 1999; Lei et al., 2008), and medicated baths (Lei and Zhang, 2005).

Extracts of *M. germanica* have promising antimicrobial (Bao et al., 2006; Kirbag et al., 2009), antiviral (Jiumei, 2001), adjuvant for arthritis in rats (Zeng 2011) and antitumor activity (Mubashir, 2011; Mubashir et al., 2010). Experimental studies showed that the leaf aqueous ethanol extract has a cytotoxic effect against breast, prostrate, and liver tumors (Nawwar et al., 2013). Moreover, the water-dissolved component of the species can improve the efficiency of the chest gland and spleen and increase immune system efficiency through the phagocytosis mechanism (Zeng et al., 2005). Some *Myricaria* species were reported to have high antimicrobial and acetylcholinesterase inhibitory activities and thus can be considered natural sources of antibiotics and drugs for the treatment of neurological disorders such as Alzheimer's disease (Mukherjee et al., 2007). All these promising properties should be further verified.

Restoration engineering use

The dense root system of the shrubs firmly anchors them in the substrate and thus reduces soil erosion (Buse-Dragomir and Niculescu, 2017; Prach, 1994). *M. germanica* is a species with great potential for plant engineering (Bonin et al., 2013) for its capacities to establish in disturbed environments and have a good resprouting (Koch and Kollmann, 2012).

Other uses

The handles of whips are made from its wood by Tartars, and it is greedily eaten by sheep, it is supposed, on account of its salty taste. It seemed to have an ornamental use in the British Isles (Loudon, 1838) and it is still found in some London gardens. In Spain it is sometimes cultivated as an ornamental in parks and gardens (Villar, 2005). The bark and other parts of *Myricaria* species yield a black dye. All plant parts, especially the bark, are rich in tannins and are used for tanning (Gaskin, 2003). In the Himalayas *M. germanica* powdered leaves and flowers are burnt as incense by some tribes (Sood et al., 2001). In Alsace, pipes are made with its branches, the marrow of which has been consumed with a hot iron wire (Cuvier, 1828). For its bitterness and astringent properties, it has occasionally been used as a tonic, and as a substitute for hops, in making beer, in Denmark (Loudon 1858) and Norway (Fuchs, 1866).

4. Cultivation

M. germanica is distributed horticulturally for its ornamental and erosion control properties. It is an easily grown plant, preferring a damp sandy soil (Thomas, 1992), fertile and well-drained, in full sun with shelter from cold drying winds, also tolerating chalky soils that are alkaline and free-draining (Huxley et al., 1992). In Siberia it is considered one of the promising genera for urban planting for its good resistance to frost, high growth rate and ornamental qualities (Lyakh, 2013).

5. Propagation for reintroduction

M. germanica can be propagated by seeds or cuttings. Seeds are sown in a cold frame to germinate and when the seedlings are large enough to handle, they are pricked out into individual pots and grown in a greenhouse or outdoors in a nursery, depending on the climate (Fig. 9).

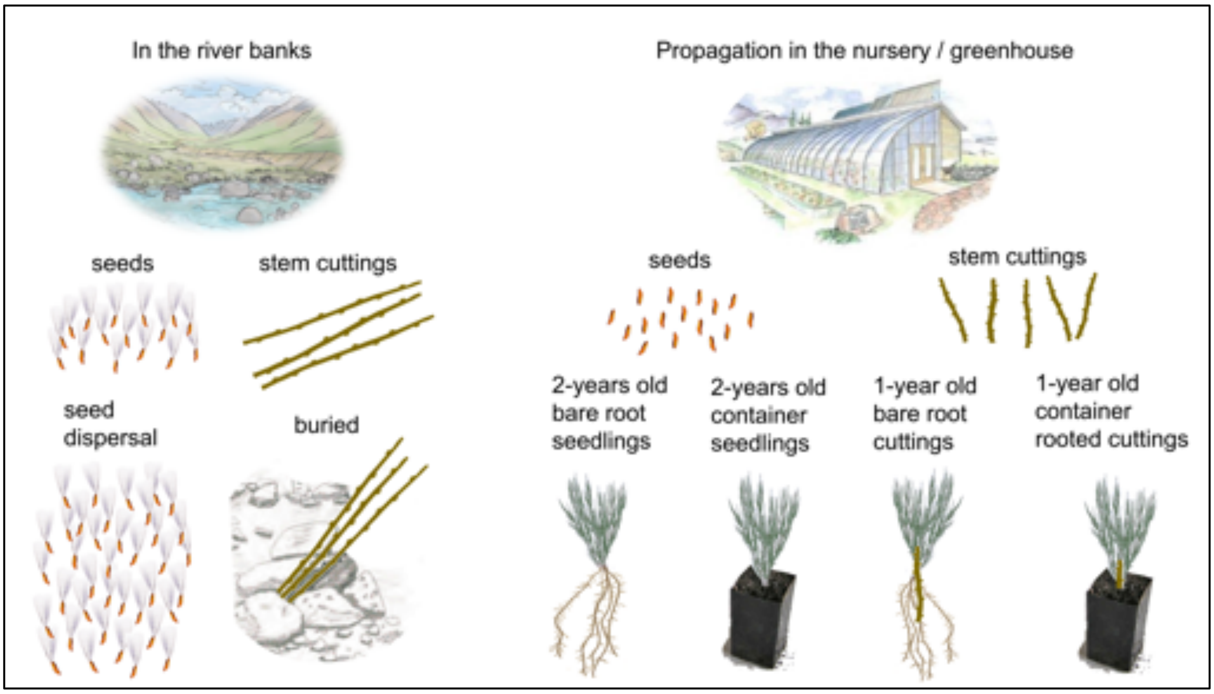

Fig. 9. ***M. germanica*** **propagation/resettlement methods (own elaboration).**

Plants are planted in their permanent positions in late spring or early summer, after the last expected frosts (PFAF, 2012). Stem cuttings can be produced in a greenhouse or outdoors in a nursery, depending on the climate. In laboratory experiments the resprouting rate after taking cuttings was 95% (Schiechtl, 1973) and 70% (Koch and Kollmann, 2012).

Cutting properties, planting depth and soil moisture play different roles for clonal propagation, including strong interactions of these factors. A cutting length of 10 cm seems suitable, and a large number of buds are helpful as roots are exclusively produced from buds. Cuttings should not be completely buried in the substrate, and at least the upper cut surface should be in contact with the air. Thus, although larger cuttings show higher survival rates, they fail if buried too deep (Koch and Kollmann, 2012). The use of container seed-derived 2-year old seedlings and secondly with 1-year old container rooted cuttings seem to be the most successful resettlement method (Harzer et al. 2018, Michielon and Sitzia, 2015).

For reintroductions, the local environmental conditions, gene pool and genetic variation of the reference area must be taken into account (Scheidegger and Wiedmer, 2014). The material for propagation should therefore be obtained from randomly selected individuals from multiple sites along the same river system (Riehl and Zehm, 2017).

6. Conservation status

M. germanica is treated as a species not yet assessed by both the IUCN Red (IUCN, 2018) and the European Commission (Bilz et al., 2011). According to EUNIS (2018), only very limited information is available about this species. However, according to our own search, it is listed in the National Red Lists and species action plans of several countries (Fig. 10).

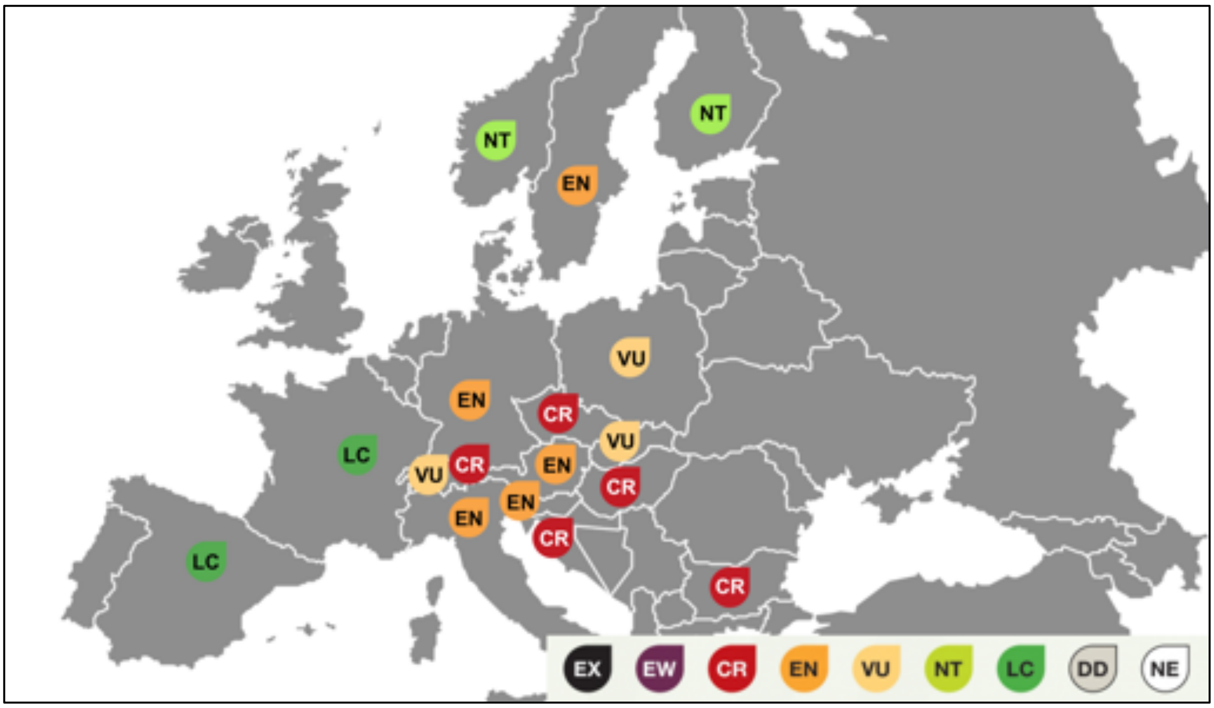

Fig. 10. Map of threat category (IUCN criteria) of *M. germanica* in European countries (own elaboration).

IUCN assesses the ecosystem German Tamarisk-Pioneer Vegetation in Europe of which the dominant vascular plant species is *M. germanica*. This ecosystem has been classified as endangered for criterion A1 (probably over 50% of losses in geographic distribution during the last 50 years), A3 (probably around 80% of losses in geographic distribution since 1750) and B2 (declines are occurring in many river systems (B2a), due to the joint effects of river channelization and hydroelectric power plant construction on vital hydromorphological processes, which may also affect occurrences downriver (B2b) (Essl, 2013).

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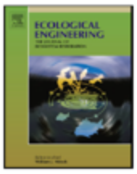

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Population dynamics of the endangered shrub *Myricaria germanica* in a regulated Alpine river is influenced by active channel width and distance to check dams

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Abstract

Despite its high conservation and indicator value, there is a lack of information on the long-term dynamics of *Myricaria germanica* (L.) Desv. (German tamarisk), and of factors affecting its population density and viability. Here we studied the dynamics of adult and juvenile *M. germanica* at 19 sites during a seven-year period (2009–2015) along a 30 km long stretch of an Italian Eastern Alpine river, by assessing a set of anthropogenic and geomorphological factors. Adult (239–571 individuals) and juvenile (62–292 individuals) population numbers showed no significant difference between years, and a remarkably uneven distribution among sites. Yet, several remnant populations have declined or disappeared in recent years and a few populations have increased. We found a positive effect of the width of the active channel on adult and juvenile plants. This means that anthropogenic river narrowing is a leading cause of the decline of the species along river banks. For juveniles, abundance also decreased with distance from downstream check dams. We conclude that in the regulated river studied, the conservation of *M. germanica* appears to be possible not only as a result of natural flow dynamics, but also at an artificial sediment storage area upstream of a check dam with a semi-natural river dynamic that maintains favourable riverine habitats. Our results are useful in a decision-making framework for the conservation of *M. germanica*, for river restoration and for flood protection in alpine valleys

1. Introduction

Natural rivers are complex and dynamic ecosystems characterized by variable biological and morphological channel structures (Richards et al., 2002; Tockner and Stanford 2002). Naturally braided rivers and their fluvial processes are characterized by a dynamic equilibrium between sediment accumulation and sediment erosion, which generates multichannel fluvial systems where sediment supply, intermittent water discharge, and bank erosion create an ever-changing mosaic of landform types (Tockner et al., 2006). In the last two centuries, natural river dynamics and morphology have been greatly modified by river control methods. A reduction in width, anastomisation and sediment transport reduction, a decrease in the ground water table and the loss of ecological connectivity are among the most negative consequences. Species typical of pioneer stages have decreased rapidly or are becoming extinct (Müller and Scharm, 2001). Natural erosion processes have been suppressed below dams, thus reducing the regeneration of pioneer species and favouring an unidirectional succession toward slower diversity (Ward and Tockner, 2001). Furthermore, channelization is having severe effects on riverine biological communities because it homogenizes habitat structure, leading to the loss of ecological niches (Meyer et al., 2013). As a result, the maintenance and restoration of hydro-geomorphic dynamics in rivers are currently considered of fundamental importance to develop a habitat mosaic and habitat features capable of supporting a variety of organisms (Gumiero et al., 2013; Ravazzolo et al., 2015). Alpine rivers host a natural flora adapted to ecotonal environmental conditions between water bodies and the floodplain, recurrently changed by fluvial processes (Camporeale et al., 2013). Riparian vegetation is a vital component of the alpine biome, because it provides breeding, resting and foraging sites for many wildlife species (Banner and MacKenzie, 1998). Riparian vegetation protects the banks against erosion (Tal et al., 2004), contributes to hyporheic water filtering and influences runoff (Tabacchi et al., 2000). Like in other regions, the natural dynamic state of most alpine streams, which sustains a diversity of successional stages, has been disrupted by anthropogenic disturbances (Ward and Tockner, 2001). Riparian ecosystems of the Alps are now among the most endangered and have been increasingly subjected to channelisation, gravel extraction and flow regulation (Müller, 1995). Nonetheless, intermediately-disturbed Alpine rivers can display an usually high heterogeneity of woody species (Sitzia et al., 2015).

Pioneer communities can be used as representative indicators not only of the hydrogeomorphic functionality of a river but also of the suitability of restoration actions, in terms of habitat diversification and increase in riparian species richness (Dufour et al., 2007). Plants found in the amphibious zone of the riparian ecosystem are adapted to harsh habitat conditions by reducing their growth rate and by taking advantage of the low availability of water and nutrients; these plants are termed stress tolerators (Grime, 1979). Müller (1995) defined these species as ‘stress-strategists’, i.e. species that cannot live in habitats other than alpine floodplains such as the pioneer perennial shrub *Myricaria germanica* (L.) Desv. (German tamarisk). *M. germanica* can grow as old as between 21 (Schweingruber et al., 2007) or 70 years (Frisendahl, 1921), but plants in the wild are usually eradicated within 15 years by periodical flooding or are outcompeted by plants of later succession stages (Lener et al., 2013). This species is therefore physiologically and morphologically adapted to stochastic events, either floods or droughts. Physiological adaptations include dispersal by wind and water, quick germination, high resprouting capacity even when buried by debris, and continuous summer blooming. The small leaf surface reduces evaporation, and the flexible branches and deep and dense root system prevent dislodging and promote drought resistance (Müller, 1995, 1998). *M. germanica* exhibits a mixed-mating system, in which both outcrossing and selfing occur (Werthand Scheidegger, 2014). Long distance dispersed seeds make this species adapted to temporal isolation (Müller, 1995, 1998). How-ever, seed germinability declines fast and the seed bank is not persistent in the soil (Müller and Scharm, 2001; Lener et al., 2013). To summarise, the biological traits of *M. germanica* make it a good indicator of natural riverine conditions, and its presence ensures that other habitats of conservation interest are in the vicinity, i.e. itis considered a keystone and flagship species (Kudrnovsky, 2013). The Alpine distribution of *M. germanica* used to be wide ranging, from lowland floodplains to mountainous riparian habitat (Kudrnovsky, 2013). In the last 150 years, its habitat extent has been constrained considerably by flow regulation with embankements, check dams and pollution, and eutrophic conditions favouring the development of competitive shrub layers, which outcompete the stress-strategist *M. germanica* (Müller, 1995; Kudrnovsky, 2013). Therefore, *M. germanica* is considered an endangered species in several national and regional red lists (e.g., Korneck et al., 1996; Rossi et al., 2013), even if it has not yet been assessed by the IUCN red list (IUCN, 2015). *M. germanica* is the dominant species of the *Salici-Myricarietum* pioneer association (Moor, 1958), which develops on gravel bars in braided alpine rivers in the temperate zone of Europe and Asia, on periodically flooded sites with silt containing fine moist sand. This association is listed in Annex I of the Habitats Directive under the 3230 code “Alpine rivers and their ligneous vegetation with *Myricaria germanica*”

(European Commission, 2013) and, as such, requires protection within the Natura 2000 network of the European Union. It is also classified as endangered by the IUCN red-list of ecosystems (Essl, 2013). *M. germanica* can reproduce easily by cuttings or seeds (Koch and Kollmann, 2012), but reintroductions have shown variable success rates (Michielon and Sitzia, 2015). The reintroduction of this species has recently been the subject of projects of national and international interest, such as in Austria (e.g., Feichtinger and Gumpinger, 2012), Germany (e.g., Koch and Kollmann, 2012), Switzerland (e.g., Rieben, 2009) and Italy (e.g., Zanichelli, 2001). The decline of this species of high conservation value is generally explained by the disruption of the river dynamic, but the role of specific anthropogenic and geomorphological determinants have not yet been quantitatively assessed. Therefore, the objective of this study was to identify factors that affect the long-term population dynamics and viability of *M. germanica*. To address this objective, we surveyed the number of adult and juvenile individuals of *M. germanica* over a seven year period (2009–2015) along a 30 km stretch of the Avisio River, a South-Eastern Alpine river where several remnant populations have declined in recent years. From each population site we measured the presence and intensity of several geomorphological and anthropogenic factors. Our hypotheses were that; (i) adults and juveniles are decreasing steadily in number of individuals with time, and (ii), variability in population size is explained by riparian ecosystem variables and the occurrence of engineering works, mainly check dams and artificial sediment storage areas.

2. Methods

2.1. General description of the study area

The study area is situated within the borders of the Avisio River catchment basin, located in Trentino, in the Italian Eastern Alps (Fig. 1). The 91.5 km long Avisio River is one of the most important tributaries of the Adige River. The Avisio drainage basin area is 940 km^2 in size, with the highest elevation at 3343 m a.s.l., including the Fassa Valleys, the Fiemme Valleys and the Cembra Valleys, and as mall part of the Pinè Plateau. The Avisio River originates at Lake Fedaia (2028 m a.s.l.) from the Marmolada glacier, flows from NE to SW, and enters the Adige River at Lavis (195 m a.s.l.), where it forms a vast alluvial plain. The river has an average gradient of 2% (Autorità di Bacino del Fiume Adige, 2008). The geological structure of the basin is mainly characterized by the effusive system formation of the Permian porphyry (porphyric Atesina platform) and by sedimentary formations of the Triassic, while the valley floor presents Quaternary sedimentary cover (Vardabasso, 1930). From a morphological aspect, the Avisio Valley represents three distinct areas: the Fassa Valley upstream of Predazzo, characterized by higher altitudes (>1000 m a.s.l.), the Fiemme Valley downstream of Predazzo, wider and of lower elevation, and the Cembra Valley, a deep and narrow gorge.

The climate is continental, with a Mediterranean influence in the most south-western part. The Avisio River is characterized by a pluvio-nival flow regime.

Over the last 25 years (1986–2010), the average discharge was 5.9 m^3s^{-1} at Soraga in the Fassa Valley, 12.9 m^3s^{-1} at Cavalese in the Fiemme Valley, and 5.5 m^3s^{-1} (this lower value is caused by hydropower utilization) at the river mouth (Bortolotti F., pers. comm., Mar., 16, 2010).

2.2. The decline of *Myricaria germanica*

General changes in the suitability of habitat conditions for *M. germanica* can be divided into three periods. The first period occurred from the end of the Little Ice Age to 1950s, and enhanced fluvial and morphological activity in the Avisio River, particularly between 1750 and 1900, like in many other alpine streams of the Alps (Rumsby and Macklin, 1996). This, coupled with low forest cover and little river manipulations, resulted in the high availability of sediment and a wide active channel. The shrubby riparian vegetation was poor due to intense animal grazing (Comiti, 2012) and firewood collection. These conditions likely resulted in arrested ecological succession of riparian vegetation, favouring *M. germanica*. The second period occurred in the 1950s when sediment-rich braided rivers, a wide active channel and reduced pressure of traditional human activities, such as grazing, allowing the growth of much shrub vegetation including *M. germanica*. The last period, since the 1960s, has been highly unfavourable for *M. germanica*, because economy expansion led to the gradual erosion of floodplains and riparian zones due to agriculture, urbanisation, industry and tourism (Comiti et al., 2011). Moreover, several disastrous floods in the past have motivated an increased need for river control measures, such as channelization, sediment mining, dams, and flow regulation (Fig. 2). Many hydraulic structures have been built along the Avisio River and its tributaries, including hydropower dams, check-dams for retention and consolidation, and bed sills. Between 1960 and 1990, active channels have been reduced in width, some dramatically so, e.g., from 250 m to 50 m (e.g. Lago di Tesero, Masi di Cavalese).

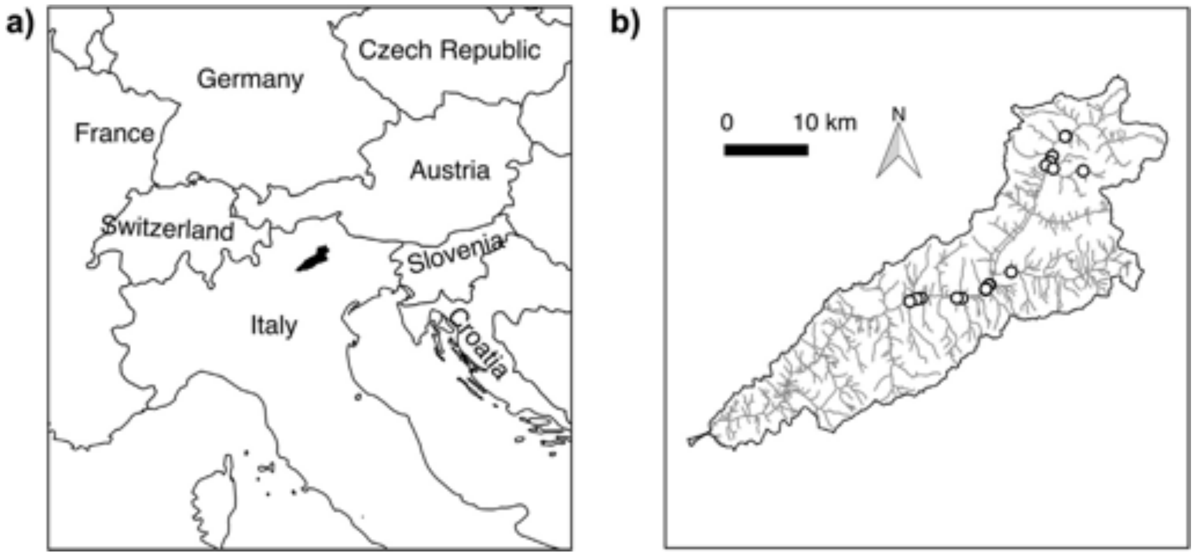

Fig. 1. Location of the Avisio River basin in Italy (a) and of the 19 surveyed population sites (b). A detailed map of site localities and other features of the river is available from the Appendix A.
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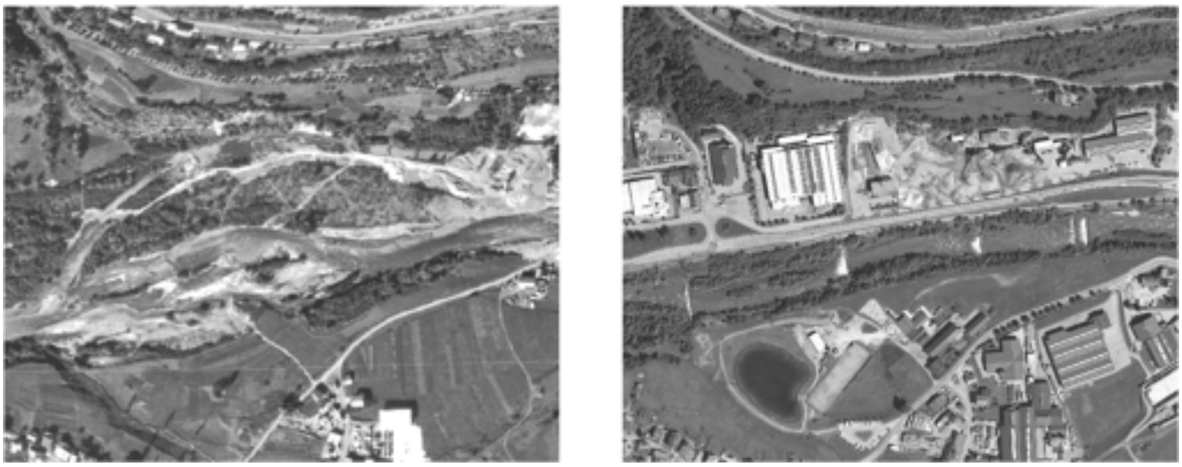

Fig. 2. Comparison between 1973 (left) and 2012 (right) aerial photos of a sub-reach of the Avisio River, at Lago di Tesero (46°17'03"N, 11°30'59"E), where human development as completely disrupted the habitat of *M. germanica*.

Some important hydroelectric dams were built along the Avisio River, generating artificial lakes (Fedaia, Soraga and Stramentizzo Lakes) and its largest tributary, the Travignolo River (Paneveggio Lake). This resulted in a degraded river, with no more gravel bars, unfavourable for the colonization of *M. germanica*. Yet, some artificially-created sediment storage areas have actually produced suitable habitats for *M. germanica*. For instance, in 1991, in order to overcome flood risk due to a very narrow section at a downstream road bridge in the village of Predazzo (seethe map in Appendix A), a 3.5 ha and 400 m long artificial sediment storage area was excavated and deepened by about 2 m (Fig. 3). This allowed for the accumulation of sediment and the maintenance of flow dynamics, which resulted in the establishment of *M. germanica* at this site since the early 2000s. *Myricaria germanica* additionally benefited from the maintenance of an ecologically acceptable river flow, which is mandatory according to Italian regulation since the1990s (Italian Law 18 May 1989, n. 183).

Fig. 3. Comparison between 1973 (left) and 2012 (right) aerial photos of the artificial sediment storage area of Predazzo, along the Travignolo River (46°18'38"N, 11°37'21"E), which has remained suitable habitat for *M. germanica* (445 individuals in 2015). The lighter and darker grey areas in the lower part of the left panel represent, respectively, gravel and woodland.

2.3. Data collection

Field surveys were carried out during the summers of 2009–2015. During the summer of 2009 the entire course of the Avisio River was systematically surveyed, from Pian Trevisan, 1690 m a.s.l., at Canazei in the Fassa Valley, to the Friendship Bridge, 460 m a.s.l., at Segonzano in the Cembra Valley, and also some of its main tributaries: the Rio di Soial and the Rio San Nicolò in the Fassa Valley; the Travignolo River and the Rio Val di Stava in Fiemme Valley. During the summers of 2010–2015 we surveyed all sites where *M. germanica* had been found in 2009 and those where the species, even if currently absent, had been recorded by previous surveys (Prosser, 2001). For each population of *M. germanica*, we counted the number of adult plants, able to bloom, and juvenile plants, immature individuals not yet blooming, which were used as response variables in the analyses. Using field observations, and cartographic and aerial photographic sources, we collected a suite of environmental data that were used as potential explanatory variables (see Table 1). Altitude was collected from a digital terrain model. From aerial photos, we measured two fundamental geomorphological variables, active channel width and river corridor width. Active channel width was defined as the moistened boundaries of the maximal flood, typically covered by gravel, and river corridor width as the boundaries of the plant communities growing near the river, influenced by river dynamics. The presence, on both banks, of river protections, and the fact that these were made with cemented boulders, were considered indicators of anthropogenic disturbance. Distance of the site centroid to the nearest upstream and downstream check dams was used to quantitatively assess the influence intensity of check dams. Finally, population site lenght parallel to the river and the occurrence of protected areas were used, respectively, as indicators of more natural conditions and institutional efforts (Table 1).

Table 1. Response and potential explanatory variables of the 19 sites (mean, maximum, minimum or frequency and standard deviation) where *M. germanica* occured along the Avisio River, North Italy.

Description	Mean (Min-Max) / Frequency	SD
Response variables		
Number of adult plants per site	21.6 (0-450)	72.9
Number of juvenile plants per site	7.8 (0-250)	31.9
Explanatory variables		
Altitude [m a.s.l.]	1,122 (845-1,760)	253
Active channel width [m]	39.2 (10-110)	27.2
Active river corridor width [m]	65.0 (12-180)	47.2
Cemented boulder bank river protection [%]	68.4	-
Bank river protection on both sides of the river [%]	94.7	-
Distance of the site centroid to the nearest upstream check dam [m]	760 (0-1,890)	617
Distance of the site centroid to the nearest downstream check dam [m]	507 (0-1,400)	375
Population site length [m]	102 (1-400)	122
Protected area [%]	31.6	-

2.4. Data analysis

We tested whether there was spatial autocorrelation between sites within the same year, using Moran's I. Our null hypothesis was that abundance values were randomly distributed across the study area. Then, we checked whether variability in abundance of adult plants was auto- and cross-correlated in space and time. Spatial synchrony refers to coincident changes in the abundances or other time-varying characteristics of geographically-disjunct population and its existence may be due to dispersal, dependence of population dynamics on synchronous stochastic effects, and trophic interactions with other species. The absence of such a synchrony between nearby population is a signal that they do not fluctuate simultaneously and some populations are likely to be abundant. This is very important for conservation because some population sites might serve to re-establish declining populations (Liebholdet al., 2004). We checked for the existence of this spatial synchrony using a Mantel correlogram for multivariate data sets (multi-year observations per site) and its statistical significance via Monte Carlo randomizations, following the procedure described by Gouhier and Guichard (2014). The Mantel correlogram shows how correlated pairs of spatial observations are when the distance (lag) between them is increased. Here it is created by computing the correlation between the time series of pairs of sites as a function of the lag distance that separates them (Gouhier and Guichard, 2014). The number of lag classes in which the maximum distance between sites is divided was set so as to have at least one site in each class.

To evaluate the effects of geomorphological and anthropogenic variables on abundance, we used Generalized Linear Mixed Models (GLMMs), assuming a negative binomial error distribution of the abundance data. Two models were performed, one on adult plants and one on the juveniles. Site was added as a random factor to account for repeated measures (i.e. sampling the same site through time). All 9 predictor variables described in the previous section were considered in these models. However, due to the extreme clumpy nature of the data and the complexity of the models, we evaluated these variables as follows. A base model was constructed including year as a fixed factor and site as a random factor. Then, one predictor variable was added at a time and its significance evaluated. Altogether, 9 models were constructed for adult plants, and 9 models for juvenile plants, with each model including year, site (as a random factor) and one of the 9 predictor variables. Results are presented for the effect of year (irrespective of its significance) and the significant predictor variables. We used the function Moran.I in package 'ape' (Paradis et al., 2004) for spatial autocorrelation within year, the package 'synchrony' (Gouhier and Guichard, 2014) for spatial synchrony analysis, and the function glmer.nb in package 'lme4' (Bates et al., 2015) for the GLMMs, all executed using the R statistical software (R Core Team, 2015).

3. Results

During the seven years survey, we identified 19 populations, 16 along the Avisio River and 3 along its tributaries. These populations varied considerably in number of plants; some become extinct, some had only few plants, and one population at Predazzo, along Travignolo River, had about 400 plants. The total number of plants in these populations varied considerably without an apparent trend between years (Table 2).

Table 2. Summary of individuals of *M. germanica* counted in 19 population sites along the Avisio River from 2009 to 2015.

	2009	2010	2011	2012	2013	2014	2015
Adults	239	285	383	571	506	457	435
Juveniles	113	229	292	130	62	107	110
Total individuals	352	514	675	701	568	564	545
Interannual difference	-	+162	+161	+26	-133	-4	-19

The abundances of plants, both adults and juveniles, present in a site were strongly influenced by the number of individuals present in the previous year (Moran's I, $p < 0.001$).

This can clearly be seen when plotting logged abundances of the populations against their spatial location in the landscape (Figs. 4 and 5). In contrast, there was no spatial autocorrelation of either adults or juveniles within each year (Moran's I, $p > 0.29$ for all years and age classes, Figs. 4 and 5). Additionally, there is no evidence of spatial synchrony in adult plants (Fig. 6). Modelling the abundances of adult plants and juveniles using year and all additional predictor variables (GLMMs) did not perform well due to the uneven distribution of abundances, i.e. two sites had very high abundances while the others were low in abundance (see Figs. 4 and 5).

As explained above, models were constructed including one predictor variable at a time. For adults, the models showed no significant difference between years (Fig. 7), but active channel width ($p = 0.007$) and active corridor width ($p = 0.053$) were significant predictors of the abundance of adult *M. germanica* plants. However, these variables were highly correlated ($r = 0.818$, $p < 0.001$), and the model including active channel width returned the lower AIC value (AIC = 630.8). In general, the number of adult plants decreased with time (not significantly), and the width of the active channel had a significantly positive effect on adult plants (Fig. 8). For juveniles, the models showed no significant difference between years (Fig. 7) and a significant effect of active channel width ($p = 0.041$). Similarly to adult plants, the width of the active channel had a positive effect on juvenile plants (Fig. 8). Further-more, the models on juveniles showed a suggestive effect of the distance of the site centroid to a downstream check dam ($p = 0.120$) (Fig. 9). The fact that downstream check dams suggestively influenced juvenile abundance, thus promoting regeneration, is probably related to the effect that check dams have on sediment deposition upstream. For instance, the artificial sediment storage area of Predazzo, approximately 100 m wide, which is upstream of a check dam, contributed to the maintenance of river dynamics and spontaneous multi-directional succession. Another artificial sediment storage area of Ziano di Fiemme, built after the disastrous floods of 1966 and approximately 1400 m long and 10 ha in size, appears to host a declining population without juveniles (70–24 individuals from 2009 to 2015), yet it is still one of the most abundant sites.

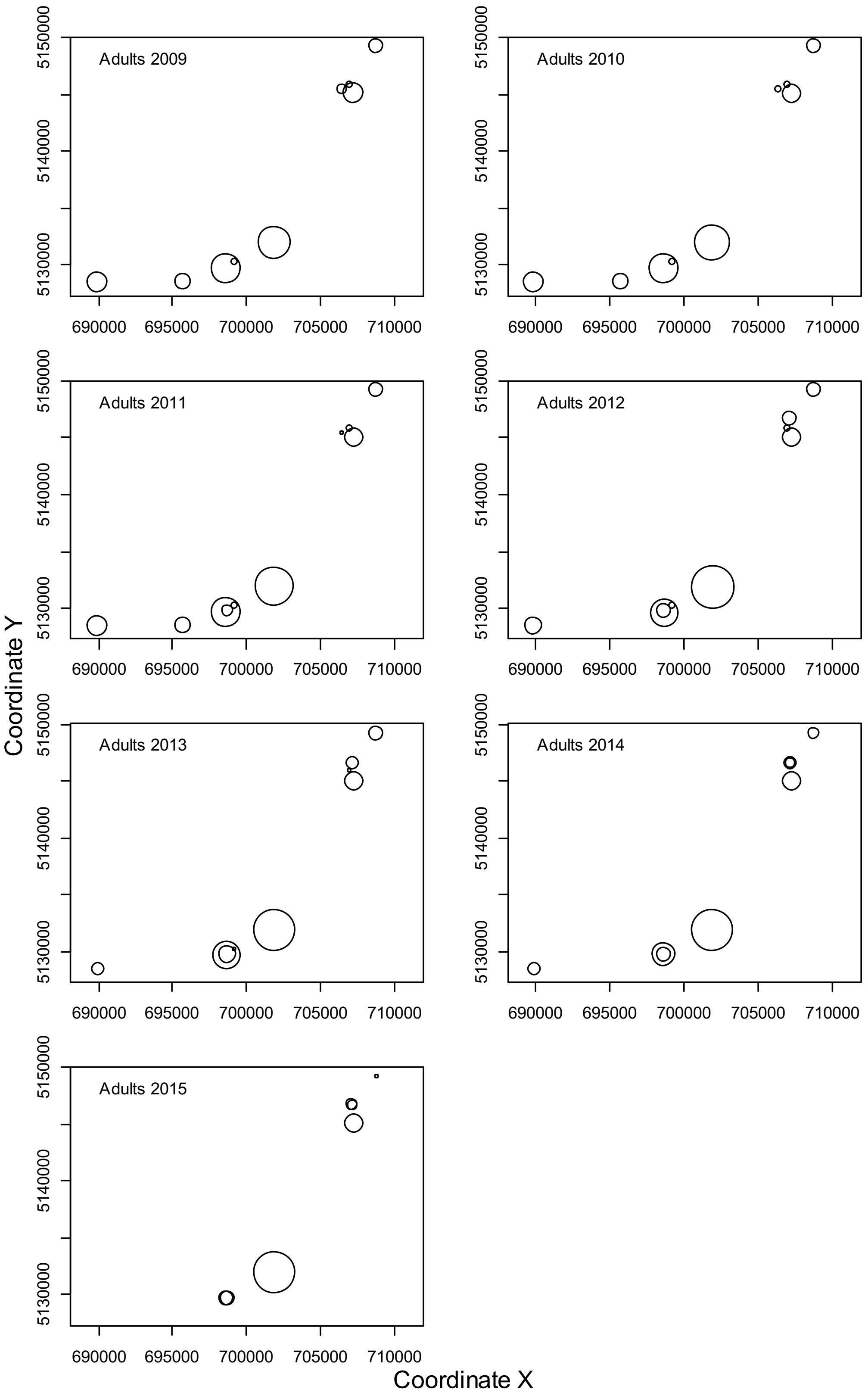

Fig. 4. Logged number of adult *M. germanica* plants plotted against geographic coordinates within the study area (coordinate reference system: ETRS89/UTM zone 32N, EPSG: 25832). The larger the circle, the higher the logged abundance at that site. The yearly plots show that the logged abundance of adult plants at a particular site is strongly influenced by the logged abundance of adult plants in the previous year (i.e., circles are of similar size at the same locality between years). Sites without individuals are not shown in the plots.

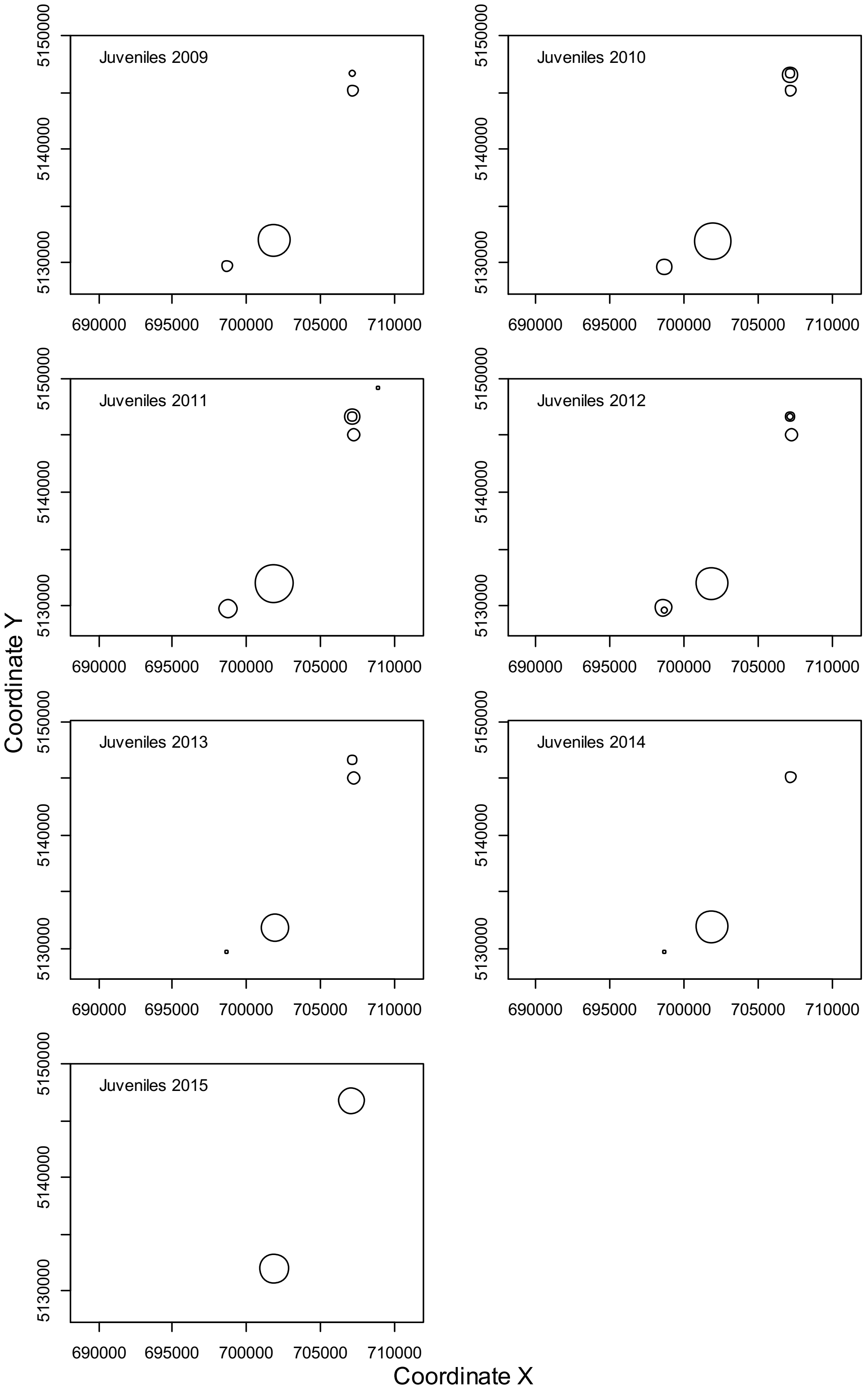

Fig. 5. Logged number of juvenile *M. germanica* plants plotted against geographic coordinates within the study area (coordinate reference system: ETRS89/UTM zone 32N, EPSG: 25832). The larger the circle, the higher the logged abundance at that site. The yearly plots show that the logged abundance of juveniles at a particular site is strongly influenced by the logged abundance of juvenile plants in the previous year (i.e., circles are of similar size at the same locality between years). Sites without individuals are not shown in the plots.

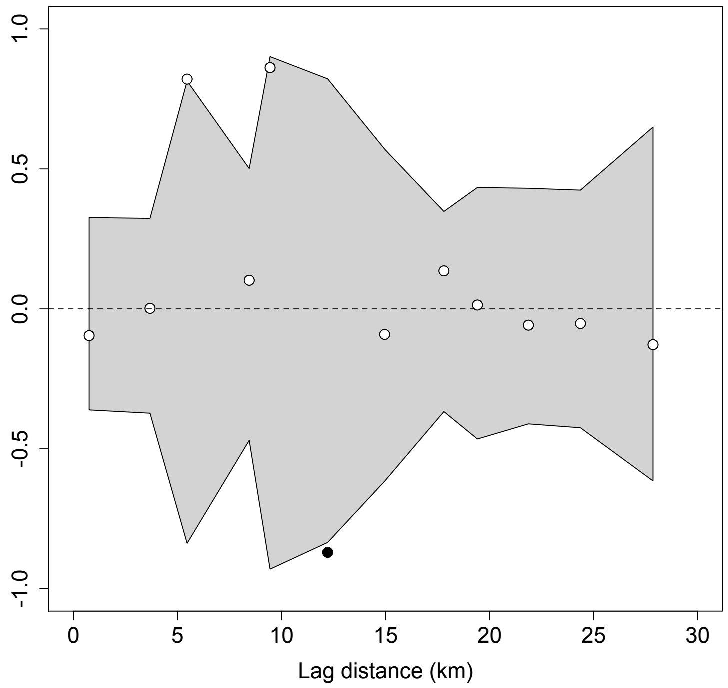

Fig. 6. Time-varying changes in the abundance of adult plants in 19 geographically disjunct populations of *M. germanica* along the Avisio River. The maximum distance (29 km) between sites was divided into 12 distance classes (lag classes). The Mantel correlogram is created by computing the correlation between the time series of pairs of sites as a function of the lag distance that separates them. The coordinates of each point on the x-axis corresponds to the average distance of sites in each lag class. Filled circles (only one here) represent statistically significant levels of synchrony ($p < 0.05$; two-tailed test) based on 999 Monte Carlo randomizations computed with the function 'vario' of the package synchrony in R, and confirm that there is no spatial synchrony, i.e. abundances do not fluctuate simultaneously. The gray region denotes the 95% confidence intervals of the Monte Carlo randomizations. The horizontal dashed line denotes the mean correlation across the entire study area.

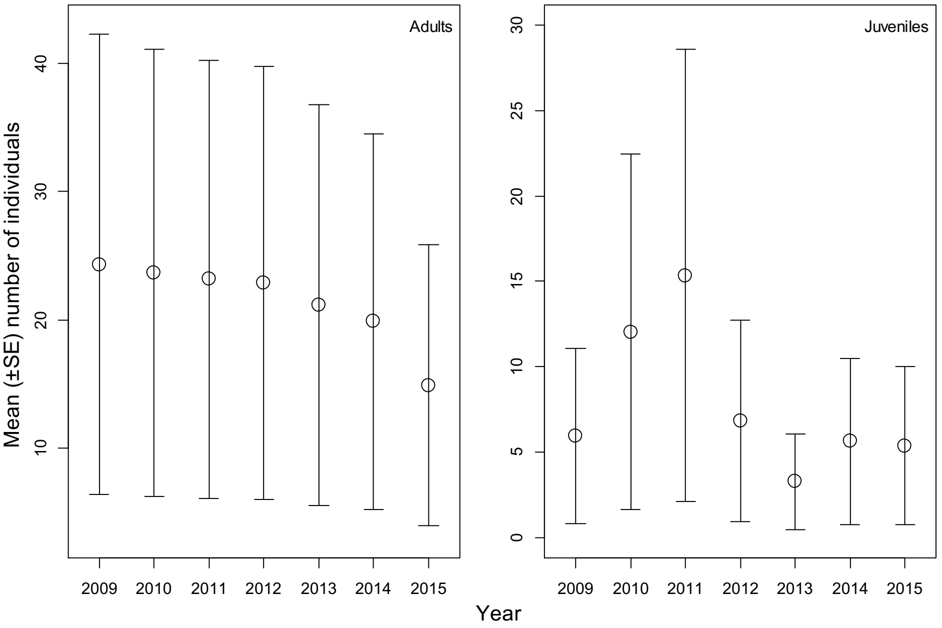

Fig. 7. Predicted (back-transformed) number of adult and juvenile *M. germanica* plants per year. The predicted values and their standard errors were calculated from the GLMMs performed.

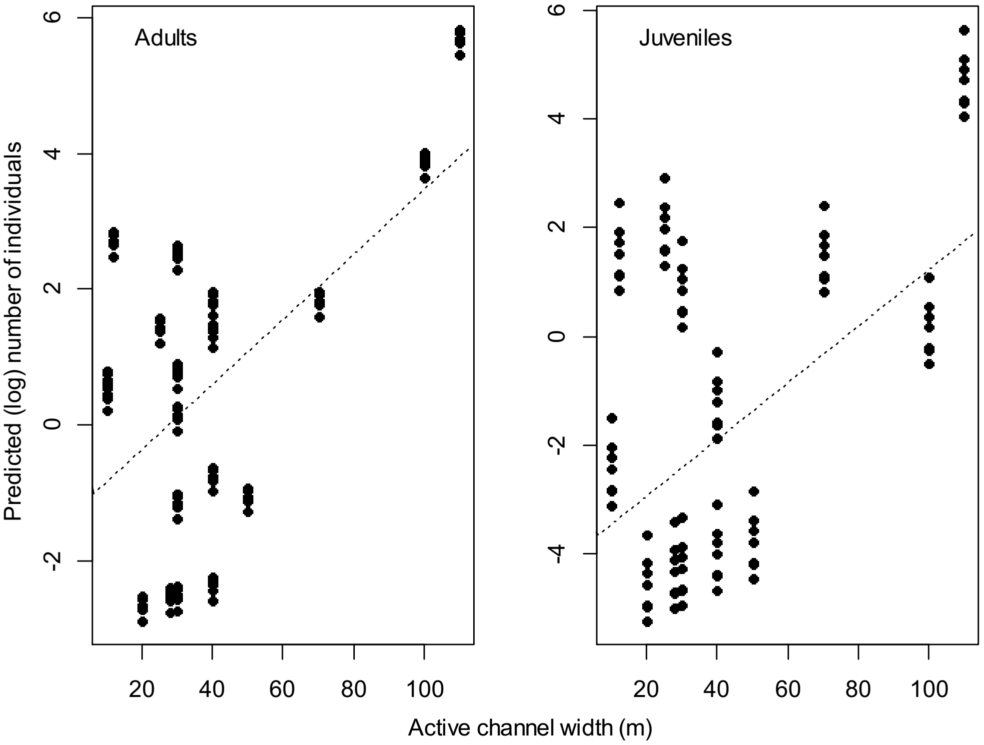

Fig. 8. The effect of active channel width on adult and juvenile *M. germanica* plants (log values). The predicted values presented here were calculated from the GLMMs performed.

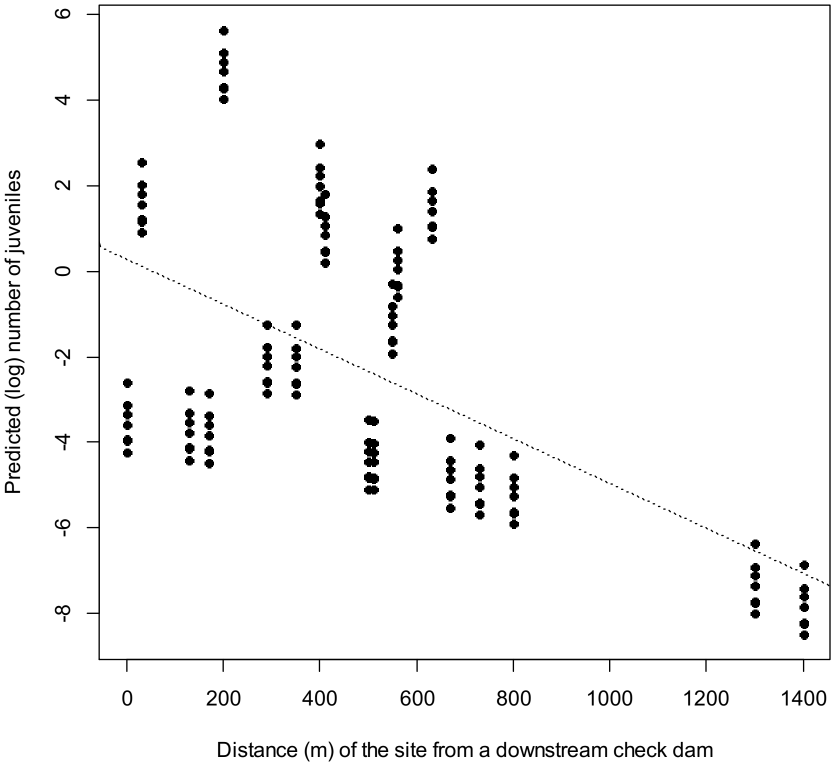

Fig. 9. The effect of distance of the site centroid to a downstream check dam on juveniles (log values). The predicted values presented here were calculated from the GLMMs performed.

4. Discussion

4.1. Population ecology of *Myricaria germanica*

The distribution and abundance of *M. germanica* is retracting in many river systems (Kudrnovsky, 2013; Kudrnovsky and Höbinger, 2015). This decline has been related to the loss of riparian wilderness in regulated rivers, i.e. the disruption of natural water flow dynamics that create new gravel bars (Tockner and Stanford 2002; Picco et al., 2016), the early-successional habitat necessary for *M. germanica* regeneration (Müller, 1998). However, these studies have either been short-term, or have not evaluated potential anthropogenic and geomorphological factors of importance to *M. germanica* abundance. We showed that adult *M. germanica* abundance is decreasing steadily in the landscape investigated and that recruitment (i.e., number of juveniles) is low, particularly in recent years. Furthermore, width of the active channel significantly affected *M. germanica* abundance, with lower adult and juvenile abundances at narrow active channels. We demonstrated that the abundances at sites in one year are reflected in the next, but that there was little evidence of spatial autocorrelation of both adult and juvenile populations within a year. Finally, we found a positive effect on juveniles based on the distance of the site centroid from downstream check dams. Due to the reduction of acute disturbances brought about by river regulation, abundances were similar across years at a particular site. Moreover, abundances of either adults or juveniles were not spatially autocorrelated between populations within years. This is in line with heterogenous environmental conditions between sites and with the differential history of populations that originated and developed under conditions that were different from the present. In the past, the connection between populations was probably higher, but today many populations are old and declining. Correlated fluctuations in species abundance can be caused by endogenous factors such as dispersal between populations and trophic interactions with species whose dynamics are spatially synchronized, or exogenous factors such as spatially-correlated environmental conditions (Liebhold et al., 2004; Gouhier and Guichard, 2014). Synchrony in the local abundance of a species can serve as an important indicator of stability and persistence. In our case, many sites are old and populations are declining, few sites are viable and increasing, and fluvial disturbances no longer periodically produce suitable habitat conditions for seedling establishment of pioneer riparian shrubs. The fact that population sites did not fluctuate simultaneously suggests differential persistence dynamics among them; if one population goes extinct the same fate is not likely to occur for the others (Liebhold et al., 2004). Adult plant abundance did not differ significantly between years, but the trend was negative for many populations. This non-significance is probably due to the rapid increase in abundance of one population, present in the artificial sediment storage area of Predazzo. The abundances of juveniles were more variable than adults, with high values in 2010 and 2011, but much lower abundances since. This variability was expected because *M. germanica* regeneration, especially in regulated rivers, is due to stochastic events, which normally do not follow a trendline. For example, the high abundances in 2010–2011 were observed in six different populations, likely due to the fact that flooding during these years brought an unusually high supply of sediment and subsequent gravel bars formation at sites with relatively wide active channels.

The width of the active channel significantly and positively influenced both the number of adults and juveniles. This corroborates existing literature about the need for wide channels to develop riparian ecosystems and in particular the establishment of *M. germanica* (Gostner et al., 2010).

4.2. Management implications

Existing conservation measures will likely not be sufficient for the survival of *M. germanica*. However, the development of sediment storage areas for hydraulic defense have paradoxically favoured the establishment of *M. germanica* in an artificial environment thanks to the greater width of the active channel, the abundance of fine sediment, the absence of hydraulic works in the active channel, and the partial restoration of river dynamics. Artificial sediment storage sites could mimic natural-like river dynamics, which is useful for the conservation of riverine pioneer habitats. Check dams, slow moving water and sediment movements have local effects on riparian vegetation and channel geomorphology. It has been shown that the accumulation of fine sediment upstream of check dams that retain soil moisture, could create a more suit-able environment for species (Bombino et al., 2014). This can be extended to the seedling establishment of *M. germanica* in a regulated river. We observed a threshold of closeness of 600 m, beyond which the positive effect of the check dam disappears. It must be noted that all the sites where this positive effect was observed were located at artificial sediment storage areas. For this reason, we expect that the planned removal of some check dams along the Avisio River will be useful for the conservation of some threatened species, like the critically endangered marble trout (*Salmo trutta marmoratus*) (Rondinini et al., 2013), but not for the conservation of *M. germanica* if an enlargement and lateral migration of the active channel will not be ensured. In fact, gravel bars necessary for the regeneration of *M. germanica* can only form in wide rivers. River widening, a river restoration strategy that allows channel movement within a spatially limited area to mitigate the effects of channelization, increases in-stream habitat heterogeneity and enhances the establishment of pioneer habitats and riparian plants (Rohde et al., 2005). The current average width of the

Avisio active channel of about 10 m in the Fassa Valley and 40 m in the Fiemme Valley is too narrow to have suitable areas for the establishment of *M. germanica* seedlings and its current populations should be considered relicts. New colonization was only observed at the 30 m wide confluence of Rio de Soial in the Fassa Valley, and in the Fiemme Valley, at 100 m wide artificial sediment storage areas. These widths allow for adequate river dynamics, while narrower channel widths may not be suitable for the long-term conservation of *M. germanica*. Moreover, the legal obligation currently in force (Italian Legislative Decree 3 April 2006, n. 152) to maintain an ecologically acceptable river flow is also a necessary condition to preserve this declining species. Given that the species did not show spatial synchrony, a planner should not be worried about the extinction of one particular population, but rather about conserving the most abundant populations capable to reproduce and disseminate.

5. Conclusions

M. germanica has been extinct for decades in all of the rivers of Trentino, except Avisio. The Avisio River, even heavily impacted, remains one of the least regulated water courses of the region, and for this reason *M. germanica* still survives. We showed that width of the active channel is currently a critical factor in the conservation of *M. germanica*. While in the short-term *M. germanica* is lively to survive, it is difficult to foresee a long-term future in a river that has lost its natural flood dynamics and where the subtraction of riverside areas eliminated suitable areas for seedling establishment. We conclude that river widening is necessary for the survival of this species and its presence can be considered a good indicator of a wide active channel river. However its long-term conservation in this area is dependent on the management of two artificial sediment storage sites and the maintenance of downstream check dams. *M. germanica* is the most characteristic species of habitat 3230 “Alpine rivers and their ligneous vegetation with *Myricaria germanica*”, protected under the Habitats Directive and assessed to be of unfavourable conservation status in the Italian alpine bio-geographical region (Genovesi et al., 2014), as well as in other alpine countries (e.g. Austria; see EEA, 2014). Our study underlines that activities such as channelisation and the modification of structures of watercourses causing active channel narrowing should be regarded as an important negative pressure to habitat 3230. The Habitats Directive and other documents of the Commission do not detail the indicators to be used in order to assess the conservation status of habitats; therefore, a number of indicators have been proposed. One indicator applied to assess the conservation status of a habitat is the abundance of individuals belonging to keystone species (Ciccarelli, 2014; Pinna et al., 2015). Indeed, *M. germanica* being the typical species of habitat 3230, should be used as a reference for this assessment at biogeographical and the

Natura 2000 site level. Hence, the abundances of adults and juveniles, coupled with active channel width relative to mean annual discharge, are valuable indicators of the structure and functions of such habitat. Future studies should evaluate whether certain engineering works aimed at the deposition of river sediments can act as surrogates of similar natural geomorphological landform types. In addition, these studies need to compare the demographics of *M. germanica* between regulated and non-regulated rivers. Monitoring the abundance of *M. germanica* for seven years might not be sufficient in highly heterogeneous and dynamic habitats such as a riparian landscape. Therefore, we encourage the application of similar or longer time frames for this and other riverine species. Moreover, data on flood discharge and sedimentation, not available in our study, could be useful to understand their influence on the different stages of the life cycle of *M. germanica*. Finally, genetic studies conducted along alpine rivers (Scheidegger and Wiedmer, 2014; Werth and Scheidegger, 2014) underline the existence of a metapopulation structure in M. germanica, which should also be investigated in the Avisio River basin.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, inthe online version, at http://dx.doi.org/10.1016/j.ecoleng.2016.06.066.

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Paper III

Short Communication

Plant population-level long-term dynamics: a case study of how a couple of years more could count

Tommaso Sitzia, Bruno Michielon, D. Johan Kotze

Abstract

Population dynamics is a field rich in theory and poor in long-term observational data. Although there are several long-term studies on population dynamics of tree species, there is a lack of studies regarding shrubs. The study of the population dynamics of the riparian shrub *Myricaria germanica* (L.) Desv. (German tamarisk) presented here is interesting and surprising.

After seven years of field surveys (2009-2015) we published the first results, now after a further three years we present new findings from this ten-year population dynamics study (2009-2018): some results are expected, others unexpected.

We have found that the adding of a few years to a longer series of population dynamics can modify the previous results. During these ten years the numbers of plants showed a remarkably uneven distribution among sites, several remnant populations have declined or disappeared in recent years and a few populations have increased. The numbers of adult and juvenile plants, mortality rate and percentage of juveniles showed a continuous change over the years.

In the first eight years we found first a population increase (2009-2012), then a decrease (2013-2016), but surprisingly, in the last two years (2017-2018) we observed a certain increase.

Keywords: German tamarisk, Demography, River restoration, Riparian habitat, Pioneer habitat, Biodiversity conservation, Natura 2000, Site of Community Importance

1. Introduction

In this work there are new findings regard the paper published:

Sitzia, T., Michielon, B., Iacopino, S., Kotze, D.J., 2016. Population dynamics of the endangered shrub *Myricaria germanica* in a regulated Alpine river is influenced by active channel width and distance to check dams. Ecological Engineering, 95, 828-838.

Improving knowledge of ecological processes is increasingly important as anthropogenic impacts affect global ecosystems. Natural rivers are complex and dynamic ecosystems characterized by variable biological and morphological channel structures and Alpine riparian ecosystems are currently among the most endangered and have been increasingly subjected to channelization, gravel extraction and flow regulation. Pioneer communities can be used as representative indicators not only of the hydrogeomorphic functionality of a river but also of the suitability of restoration actions, in terms of habitat diversification and increase in riparian species richness (Dufour et al., 2007).

Myricaria germanica is the dominant species of the *Salici-Myricarietum* pioneer association (Moor, 1958), which develops on gravel bars in braided alpine rivers in the temperate zone of Europe and Asia, on periodically flooded sites with moist sand. *M. germanica* is a good indicator of natural pioneer riverine conditions, physiologically and morphologically adapted to stochastic events, either floods or droughts and its presence ensures that other habitats of conservation interest are in the vicinity, i.e. it is considered a keystone and flagship species (Kudrnovsky, 2013).

We surveyed the number of adult and juvenile individuals of *M. germanica* over a long period along an Alpine river, where several remnant populations have declined in recent years.

The objective of the first study (field surveys 2009–2015) was to determine the trend in number of plants with time and to identify factors that affect the long-term population dynamics and viability of *M. germanica*. Currently (field surveys up to 2018) our hypothesis was also that the adding of a few years to a long time series doesn’t modify the previous results.

2. Materials and methods

General description of the study area

The study area is situated within the Avisio River basin, in Trentino Region, in the Italian South-eastern Alps. The 91.5 km long Avisio River is one of the most important tributaries of the Adige River, which flows into the Adriatic Sea.

In 2009 we selected a fluvial stretch about 30 km long in the Alps, in which we identified 19 sites, either with the presence of *M. germanica* in that year (15 sites), or where it had been extinct for no more than 10 years (4 sites). Of these 19 sites, 16 are located in the Avisio River, 3 in its tributaries.

Data collection

Field surveys were conducted every summer from 2009 to 2018. For each site we counted the number of adult plants, able to bloom, and juvenile plants, immature individuals not yet blooming, which were used as response variables in the analyses. We collected a suite of 9 environmental data that were used as potential explanatory variables: altitude, active channel width, river corridor width, presence of river protections on both banks, presence of cemented boulder bank river protection, distance of the site centroid to the nearest upstream and downstream check dams, population site length along the river, environmental protection.

Data analysis

We tested whether there was spatial autocorrelation between sites within the same year, using Moran's I. Our null hypothesis was that abundance values were randomly distributed across the study area. We then checked whether variability in abundance of adult plants was auto- and cross-correlated in space and time. Spatial synchrony refers to coincident changes in abundances or other time-varying characteristics of geographically-disjunct populations and its existence may be due to dispersal, dependence of population dynamics on synchronous stochastic effects, and trophic interactions with other species. The absence of such synchrony between nearby populations is a signal that they do not fluctuate simultaneously and some are likely to be abundant.

To evaluate the effects of geomorphological and anthropogenic variables on abundance, we used Generalized Linear Mixed Models (GLMMs), assuming a negative binomial error distribution of the abundance data. Two models were performed, one on adult plants and one on juveniles. Site was added as a random factor to account for repeated measures (i.e. sampling the same site over time). All 9 predictor variables were considered in these models, however, due to the extremely clumpy nature of the data and the complexity of the models, we evaluated these variables as follows. A base model was constructed including year as a fixed factor and site as a random factor. Then, one predictor variable was added at a time and its significance evaluated. Altogether, 9 models were constructed for adult plants and 9 for juveniles, with each model including year, site (as a random factor) and one of the 9 predictor variables. Results are presented for the effect of year (irrespective of its significance) and the significant predictor variables. We used the function Moran.I in package 'ape' (Paradis et al., 2004) for spatial autocorrelation within year, the package 'synchrony' (Gouhier and Guichard, 2014) for spatial synchrony analysis, and the function glmer.nb in package 'lme4' (Bates et al., 2015) for the GLMMs, all executed using the R statistical software (R Core Team, 2018).

3. Results

To a 7-year study (2009–2015) we added another 3 years of field surveys (2015–2018). We have thus analyzed 10 years (2009-2018) of population dynamics (Figs. 1, Fig. 2): some results are expected, others unexpected.

The number of plants in the Avisio River basin varies considerably (Table 1).

Table 1. Annual summary of individuals of *M. germanica* along the Avisio River basin.

	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Adults	239	285	383	571	506	457	435	370	375	455
Juveniles	113	229	292	130	62	107	110	90	128	93
Total individuals	352	514	675	701	568	564	545	460	503	548
Interannual difference	-	+162	+161	+26	-133	-4	-19	-85	+43	+45
Mortality rate (%)	-	3.1	5.9	6.1	29.4	15.4	14.9	33.9	8.3	8.8
Percentage of juvenile (%)	32.1	44.6	43.3	18.5	10.9	19.0	20.2	19.6	25.4	17.0

The total number of *M. germanica* plants increased from 352 up to 701 (2009-2012), decreased to 460 (2016), then increased up to 548 (2018). So adding these last 3 years to the first 7, we found an unexpected moderate recovery in the total number of plants from 2017.

If we take only two sets of annual data, between these, also with a pluriannual interval, we can see different population trends: increase, decrease, stability.

The number of sites with *M. germanica* plants was 14 (2009), increased to 15 (2010) and then decreased continuously to 9 (2018). In these 10 years human river works have had a significant impact causing the direct extinction of 3 sites and the death of several plants in 3 other sites. In all these years no river work has been performed to support the conservation of the species.

Regeneration fluctuated over the years, with an average annual number of 135 juvenile plants, a maximum of 292 and a minimum of 62. The mortality rate changed frequently: it increased up to 29.4% (2013), decreased to 14.9% (2015), increased to 33.9% (2016) then decreased to 8.3% (2017). The average percentage of juveniles also changed frequently: they increased from 32% (2009) to 45% (2010), decreased to 11% (2013), increased to 25% (2017), then decreased to 17% (2018). Other totals from these ten years are: the death of 359 adults and 321 juveniles, more than one thousand seedlings, average age of population 10 years, average age of adult plants 14 years.

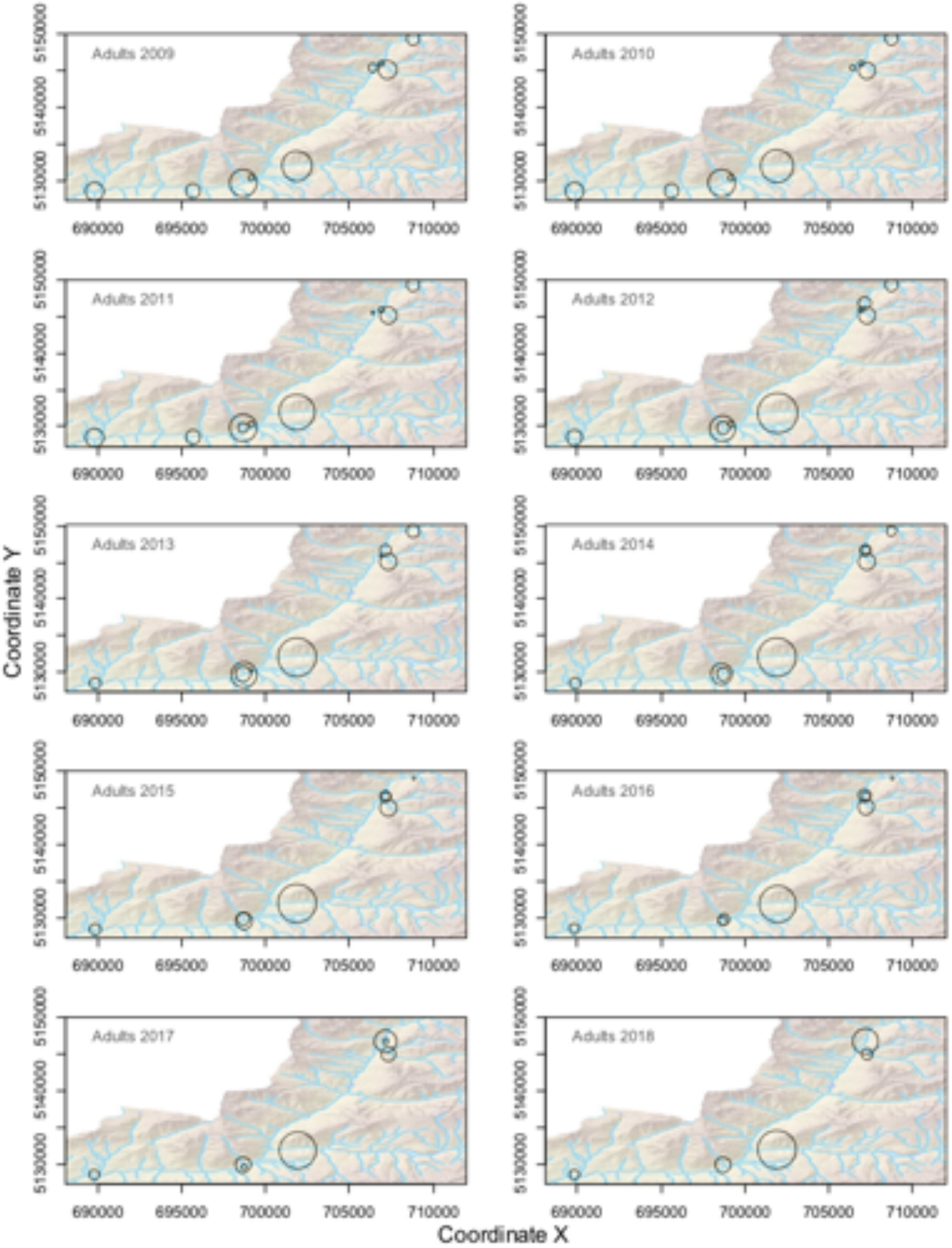

Fig. 1. Logged number of adult *M. germanica* plants plotted against geographic coordinates within the study area (coordinate reference system: ETRS89/UTM zone 32N, EPSG: 25832). The larger the circle, the higher the logged abundance at that site. The yearly plots show that the logged abundance of adult plants at a particular site is strongly influenced by the logged abundance of adult plants in the previous year (i.e., circles are of similar size at the same locality between years). Sites without individuals are not shown in the plots.

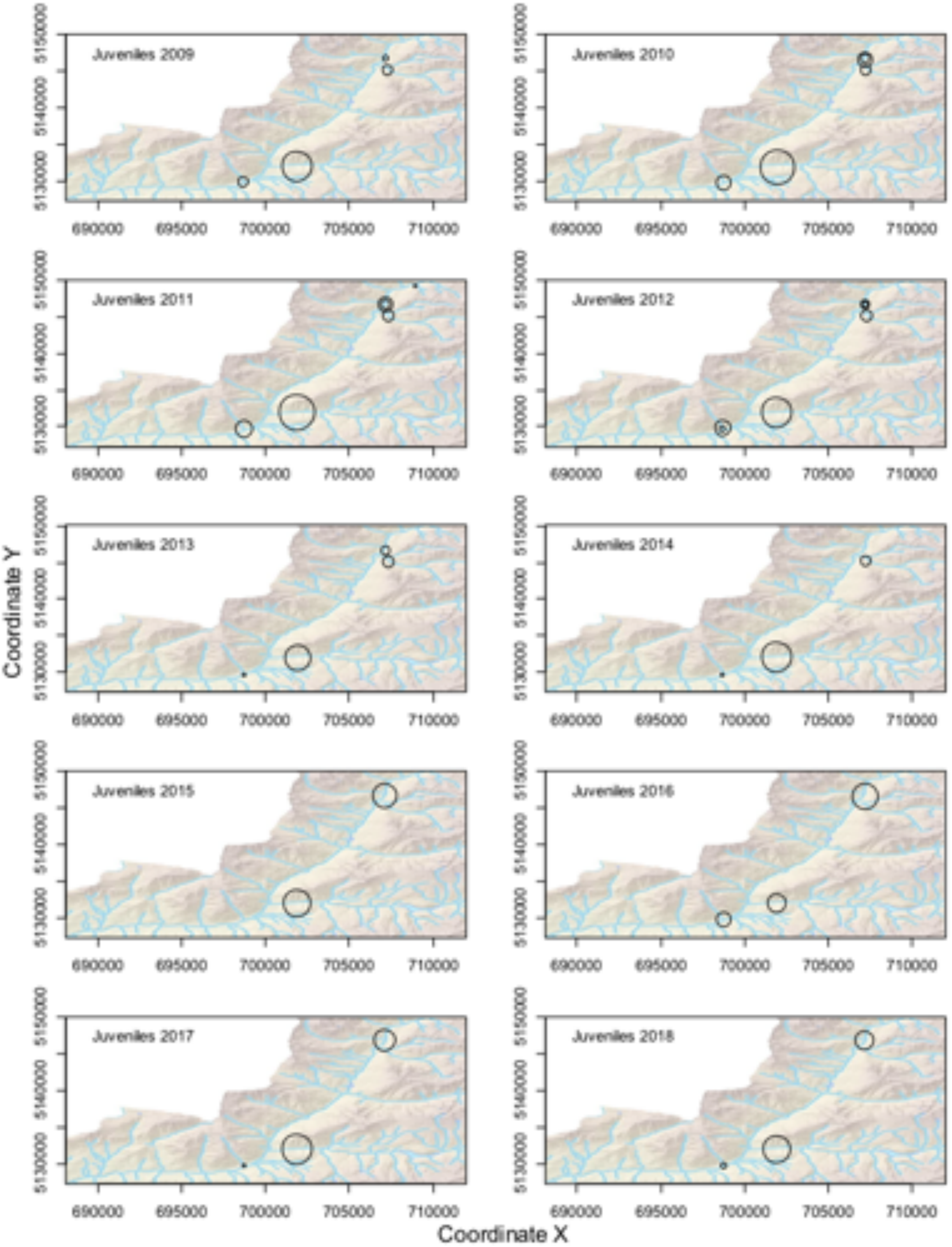

Fig. 2. Logged number of juvenile *M. germanica* plants plotted against geographic coordinates within the study area (coordinate reference system: ETRS89/UTM zone 32N, EPSG: 25832). The larger the circle, the higher the logged abundance at that site. The yearly plots show that the logged abundance of adult plants at a particular site is strongly influenced by the logged abundance of adult plants in the previous year (i.e., circles are of similar size at the same locality between years). Sites without individuals are not shown in the plots.

These highlight a dynamic population perhaps unexpected in a regulated river, with relevant and frequent human interventions. However, 99% of seedlings germinated in only three sites, two characterized by the confluence with a few small creeks, able to bring gravel sediments, and with a check dam downstream, the third, in which 80% of the seedlings germinated, is an artificial sediment storage area. Outside these three sites, less than 10 seedlings germinated in this whole period.

For adults, the models showed no significant difference between years, the number of adult plants fluctuated each year, but has not decreased, for juveniles, the models showed a high number in 2011 and no significant difference between other years (Fig. 3).

As expected, the width of the active channel and active corridor both had a significantly positive effect on adults ($p = 0.011$ and $p = 0.066$ respectively) (Fig. 4). Indeed width of the active channel and width of active corridor were highly correlated: $r = 0.818$, $p < 0.001$.

For juveniles the width of the active channel / active corridor was not significant. This seems to be due to an unexpected development of juveniles in one of the sites, without a wide active channel. This confirms the particular ecology of this species: recruitment is associated to recurrent, but somewhat unpredictable hydrological events.

Furthermore, as expected the models show a suggestive effect on juveniles of the distance of the site centroid to a downstream check dam ($p = 0.13$) (Fig. 4). This is probably related to the effect that check dams have on sediment deposition upstream.

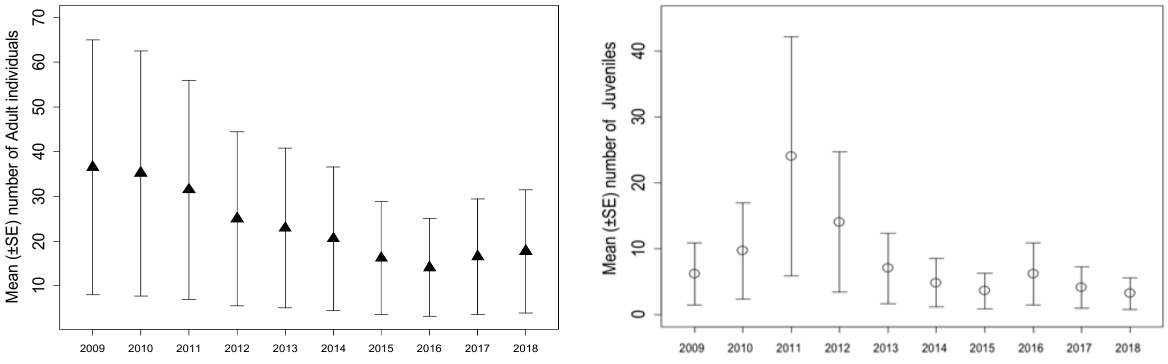

Fig. 3. Predicted (back-transformed) number of adult (on the left) and juvenile (on the right) *M. germanica* plants per year. The predicted values and their standard errors were calculated from the GLMMs.

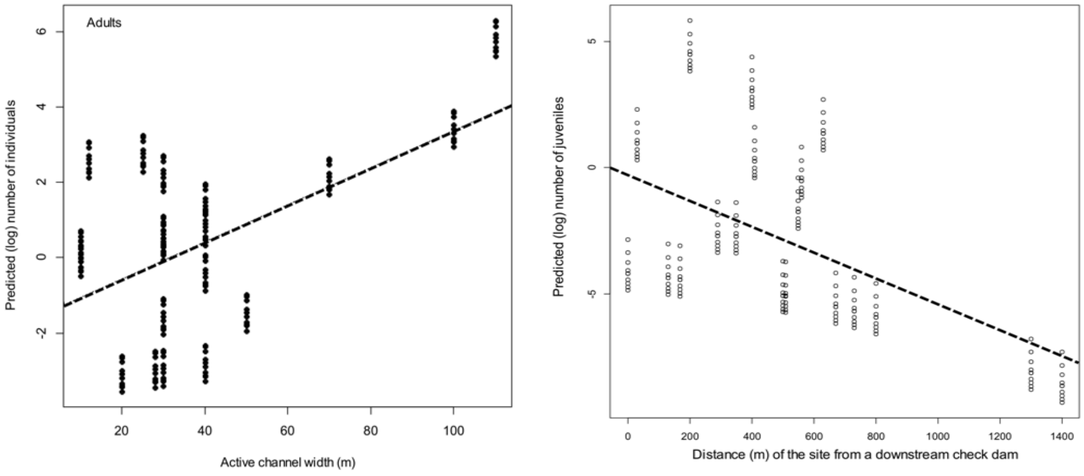

Fig. 4. The effect of active channel width on adult *M. germanica* plants (log values) (on the left). The suggestive effect of distance of the site centroid to a downstream check dam on juveniles (log values) (p = 0.13) (on the right). For both graphs the predicted values were calculated from the GLMMs.

4. Discussion

Population ecology of *Myricaria germanica*

The distribution and abundance of *M. germanica* is retracting in many river systems. We showed that, in an Alpine river basin with no specific measure for the conservation and management of *M. germanica*, the population dynamics is high, adult abundance is not decreasing and there is always a varied recruitment.

Furthermore, width of the active channel positively affected *M. germanica* abundance, significantly for adults, with fewer adults along narrow active channels. The abundances at sites in one year were reflected in the next, but there was little evidence of spatial autocorrelation of both adult and juvenile populations within a year.

Finally, a suggestive effect of the site centroid from downstream check dams on juveniles based on the distance was found.

Abundances of either adults or juveniles were not spatially auto-correlated between populations within years. This is in line with heterogeneous environmental conditions between sites and with the differential history of populations.

Correlated fluctuations in species abundance can be caused by endogenous factors such as dispersal between populations and trophic interactions with species whose dynamics are spatially synchronized, or exogenous factors such as spatially-correlated environmental conditions (Liebhold et al., 2004; Gouhier and Guichard, 2014). Synchrony in the local abundance of a species can serve as an important indicator of stability and persistence. In our case, many sites are aged and populations are declining, few sites are viable and increasing, and fluvial disturbances no longer periodically produce suitable habitat conditions for seedling establishment of pioneer riparian shrubs. The fact that population sites did not fluctuate simultaneously suggests differential persistence dynamics among them; if one population becomes extinct the same fate is not likely to occur for the others (Liebhold et al., 2004). The non-significance of the difference in adult abundances between years is probably due to the rapid increase in abundance of one population, present in an artificial sediment storage area.

The abundances of juveniles, more variable than adults, was expected because *M. germanica* regeneration, especially in regulated rivers, is due to stochastic events, which normally do not follow a trend. For example, the high juvenile abundances in 2010–2011 were observed in six different populations, likely due to the fact that flooding during these years brought an unusually high supply of sediment and subsequent gravel bars formation at sites with relatively wide active channels.

The width of the active channel had a positive and significant influence on the number of adults, positive but not significant on juveniles. This corroborates the existing literature about the need for wide channels to develop riparian ecosystems and in particular the establishment of *M. germanica* (Gostner et al., 2010).

Management implications

The current average width of the active channel in the different river stretches is too narrow for the formation of new gravel bars necessary for the establishment of *M. germanica* seedlings and many of its current populations should be considered relicts.

Existing conservation measures will likely not be sufficient for the survival of *M. germanica*, e.g. the Site of Community Importance (IT3120118 "Lago-Val di Fiemme"), designated in 2000 for the relict presence of *M. germanica*, has certainly been extinct at least since 2009 and there is no reintroduction project planned.

River widening, a river restoration strategy that allows channel movement within a spatially limited area to mitigate the effects of channelization, increases in-stream habitat heterogeneity and enhances the establishment of pioneer habitats and riparian plants (Rohde et al., 2005). However, the creation of sediment storage areas for hydraulic defense have paradoxically favored the establishment of *M. germanica* in an artificial environment thanks to the wider active channel, abundance of fine sediment, the absence of hydraulic works in the active channel, and the partial restoration of river dynamics. Check dams, located at artificial sediment storage areas, slow moving water and sediment movements, favoring the presence of moist sand, have a positive effect on seeds germination of *M. germanica*. New colonization was only observed at a wide river stretch with creek confluences and at the sediment storage areas.

Given that the species did not show spatial synchrony, perhaps planners should not be worried about the extinction of a particular population, but rather about conserving the most abundant populations capable of reproducing and disseminating. However, this remains subordinated to the dispersal capacity of *M. germanica*, generally limited to a hundred meters and only occasionally farther.

5. Conclusions

Population dynamics is a field rich in theory and poor in long-term observational data. Population dynamics theory makes important predictions that are notoriously difficult to test using short-term datasets. Although there are several long-term studies on population dynamics of tree species, there is a lack of studies regarding shrubs. The study of the population dynamics of the riparian shrub *M. germanica* is interesting and frequently characterized by unexpected events. In these ten years we have seen how a regulated stream still maintains a few river stretches with a dynamic environment, due to natural / anthropogenic causes.

Monitoring the abundance of *M. germanica* over a long period has been useful to follow its population dynamics in the riverine landscape. Only a long-term monitoring can elucidate the real dynamics characterizing riverine habitats, a discontinuous and not long monitoring can lead to inaccurate and/or wrong conclusions. The higher annual mortality rate of 29.4% (2013) and percentage of juveniles of 44.6% (2010) demonstrate the presence of high dynamics typical of a riparian environment.

We showed that width of the active channel is currently an important factor in the conservation of *M. germanica* and that river widening is necessary for the survival of this species. Moreover, data on flood discharge and sedimentation, not used in this study, could be useful to understand their influence on the different stages of the *M. germanica* life cycle.

The Habitats Directive and other documents of the Commission do not detail the indicators to be used in order to assess the conservation status of habitats; therefore, a number of indicators have been proposed. Indeed, *M. germanica* being the typical species of habitat 3230, should be used as a reference for this assessment at biogeographical and Natura 2000 site level. Hence, the abundances of adults and juveniles, coupled with active channel width relative to mean annual discharge, are valuable indicators of the structure and functions of such habitats.

Lastly, we have seen that the adding of a few years to a longer series of population dynamics can modify the previous results.

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