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TUM School of Life Sciences

Habitat configuration and metapopulations of endangered plants in Alpine rivers

How can river restoration support species conservation in a dynamic system?

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Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung einer

Doktorin der Naturwissenschaften (Dr. rer. nat.)

genehmigten Dissertation.

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Prüfer der Dissertation:

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Die Dissertation wurde am 28.03.2023 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 02.08.2023 angenommen.

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List of abbreviations

AMOVA	Analysis of Molecular Variance
ARC	Active River Corridor
DEM	Digital Elevation Model
DSM	Digital Surface Model
EDD	Effective Dispersal Distance
GBM	Gradient Boosted Machine
GI	Gravel Index
HSM	Habitat Suitability Model
LDD	Long-Distance Dispersal
RF	Random Forest
SDD	Short-Distance Dispersal
SRE	Surface Range Envelope
TIN	Triangulate Irregular Network
UAV	Unmanned Aerial Vehicles

Summary

The anthropogenic alteration of habitat quantity and quality is one of the main causes for the global loss in biodiversity. To stop the ongoing decline, conservation and restoration need an effective management of rare and threatened species, based on detailed knowledge about habitat requirements and life-cycle characteristics. In dynamic environments, such as Alpine rivers, there are particular challenges in assessing suitable sites, since many habitats are small and have a patchy distribution that varies in space and time. Spatio-temporal patch configuration and connectivity are controlled by the river dynamics and the dispersal abilities of the species, and determine the colonization success and thus the persistence of viable metapopulations. In the past two centuries most rivers and floodplains lost their former dynamics and high diversity of characteristic habitats and species due to human impacts. Therefore, river restoration is necessary to support the threatened biodiversity. Unfortunately, most restoration measures and species reintroductions achieved hardly any significant improvement in the conservation state of endangered riparian species. This is at least partly due to the small scale of most operations, and a lack of scientific understanding of the interactions between habitat dynamics and population persistence.

The PhD thesis demonstrates how analyses of habitat availability and species-specific colonization can support conservation of endangered plant species, and help restoring fragmented and dynamic river landscapes. While modelling the habitat niche and suitability of two alpine riparian pioneer plants, i.e. *Chondrilla chondrilloides* and *Myricaria germanica,* in different 'riverscapes' in the European Alps, the 'meta-habitat' configuration is combined with the species-specific dispersal abilities resulting in the calculation of the colonization potential. This is the basis for the evaluation of natural, degraded and restored riverscapes regarding habitat connectivity and their potential for supporting viable populations of the study species.

Publication 1 gives an overview of the loss and restoration of gravel bar area and thus potential habitat for pioneer riparian species. Changes in gravel bar area were assessed along five major Alpine rivers in Bavaria comparing historical maps and recent aerial images. The changes in floodplain structure over the past decades were evaluated comparing historical maps and a time series of aerial images along three degraded and five restored river reaches at river Isar. On average 80% of the former gravel bar area had been lost. The loss was accompanied by a decrease in the active river corridor and a shift from gravel-dominated to vegetation-dominated floodplain habitats. Restoration projects only partly succeeded in creation of new gravel bar area, while a large extent of the measure and intermediate flood events had a positive effect on the development of gravel bars.

Topic of **Publication 2** is the assessment of relevant habitat parameters via drone flights and derived aerial images, surface and elevation models. For a *C. chondrilloides* population within an alluvial fan in Bavaria it is demonstrated that suitable habitat can be described via vegetation cover, vegetation height and terrain height above the water table. Further, analyses of the short-term dynamics of the habitat showed a high risk of extinction for a large part of the population due to sediment erosion after heavy rainfalls. Using drones for the data assessment for modelling habitat suitability and habitat dynamics within high spatio-temporal heterogeneity proved to be a well-fitting method ensuring a high accuracy and reproducibility.

Publication 3 is a monograph on *C. chondrilloides* and comprises a summary of the findings on its historic and current distribution, morphology, taxonomy, habitat requirements, dispersal ability and conservation state. While the species was widely distributed in the north-eastern and south-eastern Alps, there were pronounced differences in the current presence of the northern and southern populations. In the northern Alps only a few and small populations remained and plants were smaller, while in the southern Alps at >100 sites large populations could be found. Detailed investigations on five selected populations revealed a rather small habitat niche of this threatened plant species, comprising relatively old sites with sparse and low vegetation at high elevation above the average water table. Dispersal distances of the species were small and seed production low, while germination rate was high. Conservation efforts are necessary, particularly in the northern Alps, and should focus on habitat restoration and reintroduction to suitable sites.

Publication 4 deals with the colonization of a recently created river stretch by a population of *M. germanica* in Engadin, Switzerland. Fourteen years after construction of the New Flaz, the structure and genetics of the established population and potential source population within the catchment were investigated to get insights in the colonization process of pioneer plants along Alpine river systems. The initial colonization was associated with a large flood event, and high diversity and distinct genetic structure of the population indicated multiple sources upstream the reach. Flood dynamics and connectivity among populations within a catchment are important prerequisites for a successful colonization of new habitats in more distant reaches. Within a river reach, colonization of arising habitat patches can be ensured by the availability of seed-producing plants in sites with less intense flood dynamics. Restoration should thus focus on habitat diversity and river continuum with natural flood dynamics.

Metrics for assessing the connectivity of different riverscapes particularly for wind-dispersed species are introduced in **Publication 5.** This study is based on the calculation of cell-based, spatially explicit measures for quantifying the colonization potential of both study species, and the connectivity given by different habitat configurations. Considering the dispersal kernel and patch configuration based on the habitat suitability models the *Effective Distance* of patches, *Number of Connections*, *Effective Connections*, and the *Connection Capacity* of the riverscape are derived and allowed conclusions on the likelihood of potential population colonization within a river reach.

In **Publication 6**, the assessment of patch connectivity according to the metrics presented in Publication 5, was applied to the two study species and five differently degraded river reaches. Identification of suitable habitat based on a habitat suitability model, from which the amount of habitat area and configuration of suitable patches are derived. Overall, *C. chondrilloides* had a smaller habitat niche, less suitable habitats available and lower colonization probability than *M. germanica.* Within the degraded river reach, habitat availability and connectivity were about 3–6 times lower than within the respective reference sites. Even slight differences in patch configuration and shape of the interface between patches resulted in considerable differences in connectivity.

The **General Discussion** summarizes and compares the findings on habitat requirements and dispersal abilities of the two study species, and evaluates the different consequences of habitat configuration on connectivity, colonization and population persistence. The current habitat situation is related to the past changes, and the relative influences of habitat loss and fragmentation is discussed for riparian pioneer plants. From these conclusions prioritization and limitations for restorations and species conservation, and implications for integrating a species-centred view in restoration planning are derived. Thus, the thesis leads from an analysis of habitat configurations and species-specific colonization processes to practical recommendations for conservation and restoration of endangered species of alpine rivers.

Zusammenfassung

Die anthropogene Veränderung der Quantität und Qualität von Lebensräumen ist eine der Hauptursachen für den weltweiten Verlust an Biodiversität. Um den anhaltenden Artenrückgang zu bremsen, ist ein wirksames Management seltener und bedrohter Spezies notwendig. Deren Erhalt und die Renaturierung ihrer Lebensräume erfordern detaillierte Kenntnisse zu den Habitatansprüchen und dem Lebenszyklus der Arten. In dynamischen Systemen, wie z.B. alpinen Flüssen, ist die Erfassung geeigneter Habitate besonders schwierig, da diese in einem sehr kleinteiligen Muster auftreten, das sich räumlich und zeitlich verändert. Die räumlich-zeitliche Konfiguration und Konnektivität der Habitatflächen in Auenlandschaften bestimmen die Besiedlungsdynamik von Populationen und damit ihre Überlebenswahrscheinlichkeit. Haupteinflussfaktoren sind die Auenstruktur, Flussdynamik und die Ausbreitungs- und Etablierungsfähigkeit der Arten. Durch menschliche Eingriffe haben in den vergangenen zwei Jahrhunderten die meisten Flüsse und Auen ihre frühere Dynamik und große Vielfalt an charakteristischen Lebensräumen und Arten verloren. Daher ist die Renaturierung von Flüssen ein wichtiger Bestandteil des Naturschutzes, um die bedrohte Artenvielfalt zu erhalten. Die meisten Renaturierungs- und Wiederansiedlungsmaßnahmen der letzten Jahrzehnte haben jedoch kaum zu einer signifikanten Verbesserung des Erhaltungszustands gefährdeter Arten der Flussauen geführt. Dies ist zumindest teilweise auf den geringen räumlichen Umfang der meisten Maßnahmen und Wissenslücken bei den Wechselwirkungen zwischen Habitat- und Populationsdynamik zurückzuführen.

Die Dissertation untersucht, wie Analysen zur Habitatverfügbarkeit und artspezifischen Besiedlungsprozessen den Schutz gefährdeter Pflanzenarten und die Wiederherstellung fragmentierter und dynamischer Flusslandschaften unterstützen können. Bei der Modellierung der Habitatnische und -eignung der beiden alpinen Pionierpflanzen *Chondrilla chondrilloides* und *Myricaria germanica* an mehreren Flussabschnitten in den europäischen Alpen wird die ‚Meta-Habitat'-Konfiguration mit den artspezifischen Ausbreitungsfähigkeiten in Zusammenhang gesetzt und daraus das Besiedlungspotenzial der Flussabschnitte abgeleitet. Dies ist die Grundlage für die Bewertung naturnaher, degradierter und wiederhergestellter Flusslandschaften hinsichtlich ihrer Habitatkonnektivität und ihres Potenzials zur langfristigen Förderung selbsterhaltender Populationen der untersuchten Arten.

Publikation 1 gibt einen Überblick über den Verlust und die Wiederherstellung von Kiesflächen und damit von potenziellem Lebensraum für die untersuchten Pionierarten. Die Veränderungen des Kiesflächenanteils wurden entlang von fünf großen Alpenflüssen in Bayern anhand historischer Karten und aktueller Luftbilder bewertet. Zur Untersuchung assoziierter Veränderungen in der Auenstruktur wurden historische Karten und eine Zeitreihe von Luftbildern der letzten Jahrzehnte entlang von drei Flussabschnitten mit unterschiedlichem Degradierungszustand verglichen. Fünf renaturierte Abschnitte wurden ebenfalls mithilfe von Luftbildzeitreihen in Bezug auf die Wiederherstellung von Kiesflächen untersucht. Die Ergebnisse zeigen, dass durchschnittlich 80 % der ehemaligen Kiesfläche verlorengegangen sind. Der Verlust ging einher mit einer Verkleinerung der aktiven Aue und einer Verschiebung von kies- zu vegetationsdominierten Auenstrukturen. Die untersuchten Renaturierungsprojekte waren nur teilweise erfolgreich bei der Entwicklung neuer Kiesflächen, wobei sich die räumliche Ausdehnung der Maßnahme und das Auftreten mittlerer Hochwasserereignisse positiv auf die Entwicklung von Kiesbänken ausgewirkten.

Gegenstand von **Publikation 2** ist die Identifikation relevanter Parameter zur Ermittlung der Habitatpräferenzen von *C. chondrilloides* mittels Drohnenbefliegung und den daraus gewonnenen Luftbildern, Oberflächen- und Höhenmodellen. Für eine Population auf einem Schwemmfächer in den Bayerischen Alpen wurde gezeigt, dass das Habitat der Art über Vegetationsdeckung, Vegetationshöhe und Geländehöhe über dem Wasserspiegel zuverlässig modelliert werden kann. Der Vergleich mehrerer Befliegungen verdeutlichte die starke Habitatdynamik und das damit verbundene hohe Aussterberisiko für einen großen Teil der Population aufgrund von Sedimenterosion nach starken Regenfällen. Der Einsatz von Drohnen für die Modellierung der Habitatansprüche und -dynamik, besonders bei hoher raum-zeitlicher Variabilität des Ökosystems, erweist sich als schnelle und einfache Methode mit hoher Genauigkeit und Reproduzierbarkeit und wird daher für die weiteren Untersuchungen in dieser Doktorarbeit angewendet.

Publikation 3 ist eine Monographie zu *C. chondrilloides*. Eine Zusammenfassung der Literatur wird ergänzt durch eigene Untersuchungen zur Morphologie, aktuellen Taxonomie, Ökologie und Habitatansprüchen der Art. Diese Daten werden komplettiert durch eine umfassende Kartierung der rezenten Vorkommen. Während *C. chondrilloides* früher in den Nordost- und Südostalpen weit verbreitet war, gibt es deutliche Unterschiede im aktuellen Vorkommen zwischen Nord- und Südalpenraum: In den Nordalpen sind nur noch wenige, kleine Populationen verblieben, bestehend aus Individuen mit kleinerem Rosettendurchmesser, während in den Südalpen an über 100 Standorten große Populationen gefunden werden konnten. Detaillierte Untersuchungen an fünf ausgewählten

Populationen ergaben eine eher kleine Habitatnische, die relativ alte Schotterterrassen mit spärlicher und niedriger Vegetation in großer Höhe über dem mittleren Wasserspiegel umfasst. Die maximale Ausbreitungsdistanz der Art liegt unter Normalbedingungen bei rund 14 m. Pro Pflanze werden verhältnismäßig wenige Samen produziert (im Schnitt rund 250), während die Keimungsraten mit >90% hoch sind. Insbesondere in den Nordalpen ist der Erhaltungszustand kritisch und Erhaltungsmaßnahmen dringend erforderlich. Diese sollten sich auf die Wiederherstellung von Habitaten und auch die Wiederansiedlung an geeigneten Standorten konzentrieren.

Publikation 4 befasst sich mit der Besiedlung eines neu angelegten Flussabschnitts im Engadin (Schweiz) durch *M. germanica*. Vierzehn Jahre nach dem Bau des *Neuen Flaz* wurden die Struktur und Genetik der etablierten Population und möglicher Quellpopulationen im Einzugsgebiet untersucht, um Einblicke in den Besiedlungsprozess von Pionierpflanzen entlang alpiner Flusssysteme zu erhalten. Die Erstbesiedlung stand im Zusammenhang mit einem großen Hochwasserereignis, und die hohe Diversität und die andersartige genetische Struktur der Population deuten auf mehrere Ursprungspopulationen flussaufwärts des Einzugsgebiets hin. Die Hochwasserdynamik und die Konnektivität zwischen den Populationen innerhalb eines Einzugsgebiets sind wichtige Voraussetzungen für eine erfolgreiche Besiedlung neuer Habitate in weiter entfernten Abschnitten. Innerhalb eines Flussabschnitts kann die Besiedlung neu entstehender Standorte durch das Vorhandensein von samenspendenden Pflanzen außerhalb der häufigen Flussdynamik gewährleistet werden. Bei der Renaturierung sollte daher auf die kleinräumige Habitatvielfalt und die longitudinale Durchgängigkeit fokussiert werden, wobei die Bedeutung der Hochwasserdynamik für die Fernverbreitung von Diasporen berücksichtigt werden sollte.

Neue Indices zur Bewertung der Konnektivität verschiedener Flussabschnitte für windverbreitete Arten werden in **Publikation 5** vorgestellt. Deren Berechnung basiert auf der zellbasierten, räumlich expliziten Quantifizierung des Besiedlungspotenzials der beiden untersuchten Arten und der durch verschiedene Habitatkonfigurationen gegebenen Konnektivität innerhalb von Flussabschnitten. Auf der Grundlage der Habitateignungsmodelle und des Ausbreitungskernels der Arten werden *Effective Distance* der Habitatflächen, *Number of Connections*, *Effective Connections* und die *Connection Capacity* für die Flussabschnitte abgeleitet. Die Indices erlauben Rückschlüsse auf die Wahrscheinlichkeit einer potenziellen Besiedlung innerhalb eines Flussabschnitts und den direkten Vergleich der Konnektivität verschiedener Habitatkonfigurationen. Im Vergleich zu bisherigen Konnektivitätsindices berücksichtigen die hier entwickelten die Spezifikationen von Samenausbreitung an Flüssen, unter anderem durch die Berücksichtigung der Abnahme der Samendichte mit der Entfernung zur Mutterpflanze und der Bedeutung des Interfaces zwischen Patches für den Samenaustausch.

In **Publikation 6** wird die Bewertung der Patch-Konnektivität anhand der in Publikation 5 vorgestellten Metriken auf die beiden untersuchten Arten und fünf unterschiedlich degradierte Flussabschnitte angewendet. Die Identifizierung geeigneter Lebensräume basiert auf einem *Habitat Suitability Model*, aus dem die Konfiguration der geeigneten Habitatflächen abgeleitet wird. Insgesamt zeigte *C. chondrilloides* eine kleinere Habitatnische, weniger verfügbare geeignete Habitate und eine geringere Besiedlungswahrscheinlichkeit als *M. germanica*. Innerhalb der degradierten Flussabschnitte war die Verfügbarkeit und Vernetzung von Habitaten etwa drei- bis sechsmal geringer als in den jeweiligen Referenzgebieten. Aufgrund geringer Ausbreitungsdistanzen führten selbst geringe Unterschiede in der Konfiguration zu erheblichen Unterschieden in der Konnektivität.

In der allgemeinen **Diskussion** werden die Ergebnisse zu den Habitatanforderungen und Ausbreitungsfähigkeiten der beiden untersuchten Arten zusammengefasst und verglichen sowie die unterschiedlichen Auswirkungen der Habitatkonfiguration auf die Vernetzung, Besiedlungspotential und Etablierung von Populationen bewertet. Die aktuelle Habitatsituation wird mit den historischen Veränderungen von Auenstruktur und Kiesflächen in Beziehung gesetzt und die relativen Einflüsse von Habitatverlust und -fragmentierung diskutiert. Aus diesen Schlussfolgerungen werden Prioritäten und Limitierungen für die Renaturierung von Auenhabitaten und den Artenschutz abgeleitet.

Es wird die Integration eines artenzentrierten Ansatzes in die Renaturierungsplanung empfohlen und die Übertragbarkeit des methodischen Ansatzes auf weitere Ökosysteme diskutiert. So führt die Arbeit von der Analyse der Habitatkonfigurationen und artspezifischen Besiedlungsprozesse zu praktischen Empfehlungen für den Schutz und die Wiederansiedlung gefährdeter Arten an alpinen Flüssen.

GENERAL INTRODUCTION

Biodiversity loss and habitat decline

Habitat destruction is one of the main drivers for biodiversity decline worldwide (Chase et al., 2020; Horváth et al., 2019). The transformation of habitats generally consists of three components, i.e. degradation, area loss and fragmentation, and there is an ongoing discussion about their relative importance and interactions (Banks-Leite et al., 2020). All together the three factors have negative effects on the persistence of populations and therefore on the occurrence of a species within its distribution range. While habitat loss reduces population sizes more or less directly, due to the species-area relationship (Horváth et al., 2019), it also leads to a fragmentation of the remaining patches. Fragmentation and lower habitat quality affect population viability in terms of altering functional connectivity between populations, thus, reducing fitness of individuals and genetic diversity, and leading to higher extinction risks (Mortelliti et al., 2010; Swift and Hannon, 2010). Under ongoing habitat loss, there may arise a threshold, when fragmentation effects exceed those of the decrease in habitat amount (Swift and Hannon, 2010; Chase et al., 2020). Particularly at intermediate levels of habitat losses, the spatial configuration of habitat fragments has a great influence on population persistence, while responses of populations to these configuration changes are species-specific (Parker and Mac Nally, 2002; Villard and Metzger, 2014).

Habitat restoration and species conservation

Applied ecology has developed two types of approaches to counteract the species decline following habitat destruction: i) habitat restoration as part of ecological restoration, and ii) species conservation encompassing the management of protected areas and management of remnant (threatened) populations (cf. Questad et al., 2014; Volis, 2019). Habitat restoration deals with the improvement of site conditions or increase in the habitat availability for a certain species. Goals and kind of measures act at different scales and reach from restoration of single patches to enhance local populations, up to the establishment of large landscape structures to increase connectivity among populations (Miller and Hobbs, 2007).

However, dispersal limitations hamper recolonization of extinct or restored patches, and thus expansion of a population (Volk et al., 2018). To overcome these limitations and to support small and isolated populations at risk of extinction, assisted colonization or reintroduction are used in conservation (Seddon, 2010). However, several reintroduction projects had a high degree of failure, due to the selection of habitats that were unsuitable (Diekmann et al., 2015; Godefroid et al., 2011). This underlines the importance of i) detailed analysis of habitat requirements of the target species, also for ii) restorations that should not only focus on the recovery of degraded ecosystems, but explicitly on the re-establishment of appropriate habitat conditions, and iii) assessing the potential of spatio-temporal patterns in seed dispersal before site selection and restoration planning (Török et al., 2018). Further, strategic restoration planning can help to overcome dispersal limitations: linking fragments by restoring corridors increase species persistence rates up to 24%, almost reaching effects of fully restored landscapes (Renton et al., 2012).

Hence, both restoration and conservation become more effective in counteracting biodiversity declines by carefully considering habitat requirements and spatial demands of the respective group of endangered species depending on their colonization potential (Metzger and Brancalion, 2016; Volis, 2019). For this, linking habitat suitability to dispersal models for assessing potentially colonisable habitats with conservation and restoration relevance at a landscape scale can be a promising method (Miller and Hobbs, 2007; van Loon et al., 2011). These species-centred approaches are highly recommended, if supporting target species or augmenting populations of endangered species groups is the goal of the restoration actions (Pander and Geist, 2013).

A metahabitat approach

The thesis ties in with the conception of Kirchhoff et al. (2013) in the field of landscape ecology, referring to an organism-centred approach, described by the term 'meta-habitat ecology' (Glossary see Box 1). The metahabitat comprises the part of a landscape that builds the environment for a certain species, rather focusing on habitat patterns and processes than on analyses of general landscape structures and changes. The base is the definition of 'habitat' for a species, that is restricted to patches, i.e. discrete areas with a certain degree of suitability surrounded by a (unsuitable) matrix. Like in metapopulations, each patch shows certain dynamics between emergence (=colonization), destruction (=extinction), or changes in quality, e.g. through succession (=demographic changes). Moreover, there is a minimum patch size and a minimum life time, to be available for species colonization. It can be assumed that there is a critical range of spatio-temporal patterns in patch arrangement for a certain species, resulting in viable metapopulations (e.g. Reich, 1991; Stelter et al., 1997). I refer to this processes as 'metahabitat dynamics', that describe the changes in habitat configuration, organism-centred, but independent of the presence of a real metapopulation. Thus, dynamic and patchy landscapes can be assessed for their potential of supporting metapopulations of a target species. This concept is a promising approach within landscape ecology to identify measures for restoration and conservation to support rare and threatened species.

Colonization in metapopulations

'Colonization' is defined as the establishment of seedlings on a suitable but unoccupied site. So, seed dispersal, germination ability and seedling growth drive successful colonization in regional plant populations (Soons and Heil, 2002). Colonization represents a central process in metapopulation dynamics, antagonistic to local extinction, ensuring population persistence on the long-term. The classical metapopulation approach assumes a balance between colonization and extinction of discrete habitat patches (Hanski, 1998), where extinct patches remain suitable and can be recolonized. In natural environments, extinction is mainly caused by the population response to unsuitable conditions. 'Unsuitable' in a wider sense mean the destruction of a patch through catastrophic events, e.g. floods, or due to a slow turnover to low habitat quality, e.g. by succession. Thus, events that precede colonization have to be considered in the metapopulation assessment. Successful colonization of unoccupied but suitable patches is assumed to be the most important and critical step to ensure survival of (meta-)populations. The connectivity-dependent colonization is affected by i) spatio-temporal habitat configuration, and ii) species-specific dispersal abilities (DeWoody et al., 2005). While habitat dynamics, i.e. catastrophic events, leads to the development of new suitable patches, that later can be colonized (Thomas, 1994), colonization relevant characteristics, i.e. dispersal, germination, seedling growth drive the population dynamics of a certain plant species within a given habitat configuration (Bossuyt and Honnay, 2006).

Box 1. Glossary of population, habitat and landscape characteristics in alpine riparian zones

Available habitat	Product of habitat area and patch connectivity (Pascual-Hortal and Saura, 2006)
Colonization	Establishment of seedlings at suitable but unoccupied patches via migration (re-colonization from seed bank excluded) (after Soons and Heil, 2002)
Colonization potential	Probability of a plant species to establish on patches at a given habitat configuration independent of the actual patch occupancy; a function of patch connectivity and establishment rate (germination, seedling survival) of the species
Dispersal kernel	A probability density function of the location of seed deposition with respect to the source (Nathan and Muller-Landau, 2000)
Habitat	Riverscape areas, which meet the specific combination of environmental conditions that is required by individuals of the study species (after Miller and Hobbs, 2007)
Habitat configuration	Spatial arrangement of habitat patches at a given time (Villard and Metzger, 2014)
Landscape connectivity	The degree to which a landscape facilitates dispersal of individuals and genes (Zeller et al., 2020), depends on river-specific dynamics
Metahabitat	Sum of dynamic connected actual and potential patches, that change over space and time, in contrast to the static 'available habitat'
Metapopulation	Spatially structured cluster of populations within a network of habitat patches (→ Metahabitat) in which species occur as discrete local populations connected by dispersal and undergoing extinction and colonisation (after Hanski, 1998)
Patch	Distinct areas of the habitat of a species arranged in a certain landscape
Patch connectivity	The degree to which dispersal between habitat patches is supported, depending on distance, size, shape of patches, matrix conditions and dispersal abilities (→ Colonization potential) (after Prugh, 2009)

Habitat availability and colonization potential

The combined effects of habitat configuration and the species-specific dispersal and establishment characteristics (Metzger and Brancalion, 2016; Pascual-Hortal and Saura, 2006; Tischendorf and Fahrig, 2000) are evaluated to investigate the colonization probability within a given landscape, that determines population persistence (cf. Fig. 1.1). The habitat that is reachable for individuals of a population to a certain time, and thus of relevance for the colonization processes, is defined as 'available'. It depends on the connectivity of habitat patches and is a function of landscape and species characteristics. Habitat availability is investigated from the identification of suitable habitat, species' colonization potential and habitat configuration and connectivity.

Habitat suitability

In the first step of assessing species' requirements on site conditions and their spatial arrangement, 'habitat' for a certain target species has to be defined. For classifying the landscape in site conditions that are suitable (=habitat) or unsuitable (=non-habitat or matrix) for living and reproduction of a species, *Habitat Suitability Models* (HSM) are frequently applied (Hirzel and Le Lay, 2008). To predict habitat suitability across a landscape, these models connect known locations of the species and spatially explicit data on environmental conditions that are expected to determine species distribution (Gogol-Prokurat, 2011). There are several methodological approaches in calculating HSMs, i.e. profile, statistical and machine-learning approaches. For instance, the *Surface Range Envelope* method (SRE, profile approach) results in explicit ranges of the input environmental variables under which the species occurs with a defined probability, that can be further defined as 'suitable'. More recently, machine-learning modelling, such as *Gradient Boosting Machine* (GBM) or *Random Forest* (RF) contributed to a further improvement in the accuracy of habitat predictions (Rew et al., 2020). Over the past years, development of remote sensing technology substantially improved the precision of input data for the models, while still limitations remain, such as high costs or poor spatio-temporal resolution (Rew et al., 2020). Today, the assessment of small-scaled ecosystems or patchy and dynamic environments, e.g. in wetlands, benefit from the increasing use of drones (unmanned aerial vehicles, UAV) for environmental data assessment, that can overcome those limitations and additionally reduce labour expended surveying and sampling on the ground (Dronova et al., 2021; Gómez-Sapiens et al., 2021), further improving habitat modelling.

Colonization process

Secondly, the species-specific potential to colonize patches of a particular habitat configurations is investigated including dispersal abilities and establishment process. The spatial pattern of seed dispersal can be described by a dispersal kernel that provides the proportion of seeds reaching a certain distance from the mother plant (Clark et al., 1999). Clark et al. (1999) further defines the 'seed rain' of a plant as function of dispersal kernel and fecundity (rate of seed production), that lead to an estimation of the real seed density from the parents. The distance over which plants disperse seeds depends on plant traits, dispersal syndrome and environmental conditions with spatio-temporal variation (Vittoz and Engler, 2007). For example, seed size (small seeds disperse further than large seeds) and release height (tall species disperse further than short ones) show influences on dispersal distance particularly for wind-dispersed species (Thomson et al., 2011). The majority of seeds are only dispersed over a few meters from the source, and long-distance dispersal (LDD) events are rare and hard to predict (Nathan et al., 2008). Compared to the regular dispersal (short-distance dispersal, SDD) with mainly local effects on populations, LDD plays an important role in the flow of individuals between populations and colonization of unoccupied habitats especially in fragmented landscapes where patches are more isolated (Nathan et al., 2002; Schurr et al., 2009). After dispersal to suitable patches, the establishment rate of a species drives the actual colonization success. Plant species are often seed limited, but establishment limitation can even be stronger than seed limitation (Clark et al., 2007). Establishment is a function of germination rate, seedling survival and the transition rate to maturity (Stöcklin and Bäumler, 1996), while early-life stages are considered to be most sensitive to environmental impacts (Clark et al., 2007).

Habitat configuration and connectivity

In a third step, after classifying the respective landscape in 'suitable' and 'unsuitable' patches (and potentially intermediate stages), the spatial arrangement of patches can be characterized by different indices, such as habitat amount, size, shape, distance, density and connectivity (Metzger and Brancalion, 2016). 'Connectivity' can be defined as the degree to which dispersal occurs between patches, and can either be used as a patch attribute ('patch connectivity') or property of an entire landscape ('landscape connectivity') (Kindlmann and Burel, 2008). Connectivity is a species-specific concept as it refers to the dispersal ability of the respective species. Most connectivity metrics are developed for assessing animal movement and metapopulation dynamics in fragmented landscapes (Keeley et al., 2021). Hence, the mostly used node-link concept (Saura and Pascual-Hortal, 2007) rarely consider the special case of plants. For example, sessile organisms with a certain dispersal kernel reachability of other patches are influenced by their position within the patch, thus edge-to-edge distances and the interface between patches must be considered for calculating seed exchange, that is relevant for colonization (P5). Further, in dynamic systems connectivity can vary over time and there might exist connectivity windows, with higher probabilities of colonization between patches (Zeigler and Fagan, 2014), implicating the consideration of spatio-temporal connectivity analysis.

However, connectivity measures are important tools in conservation planning (Keeley et al., 2021) and are also the best landscape indicator for restoration success, since they combine data on habitat amount, arrangement and species dispersal characteristics (Metzger and Brancalion, 2016). The connectivity measures reflect the probability for a species to colonize suitable habitats and must be seen as configuration attribute. For calculations on real colonization rates or population dynamics, data on population sizes, fecundity, germination rates and demographic processes must be included in modelling.

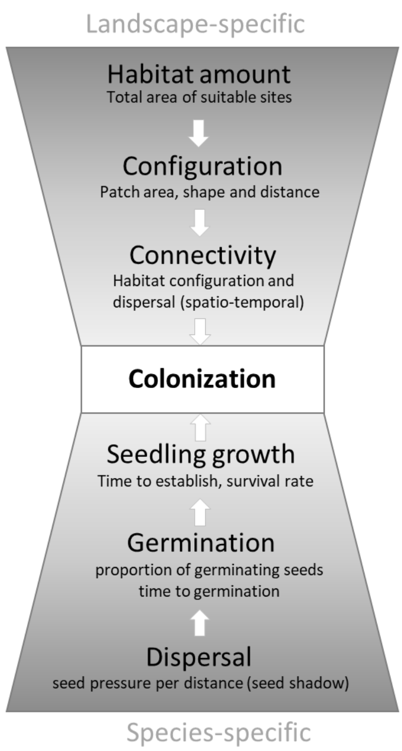


Figure 1.1 Overview on the variables that influence colonization within plant populations in gravel rivers. While landscape components, like habitat amount, configuration and connectivity influence habitat availability for a species, species-specific life-cycle characteristics affect the sensitivity to changes in habitat availability. A central driver of population persistence in a landscape are successful colonization events that can be impacted by altered habitat availability, while the degree depends on the species dispersal abilities and establishment rate.

Alpine rivers as dynamic model systems

For analysing the consequences of anthropogenic alterations in habitat configuration, metapopulation concepts are widely used, although they were originally developed for natural patchy environments, e.g. dynamic systems with frequent disturbances (Hanski, 1998; Keymer et al., 2000; Wiens, 1997). While in classic metapopulation models colonization and extinction rates mainly depend on migration rates and demography, in real (dynamic) environments extinction on patches is mostly accompanied by their transformation from suitable to unsuitable through disturbances, and vacated patches are not automatically available for recolonization (Thomas, 1994). So the creation and destruction rates of habitat patches drive the (colonization and extinction) dynamics in these metapopulations, also described as 'patch dynamics' (cf. DeWoody et al., 2005) or here metahabitat dynamics. Thus, studying metapopulations in dynamic systems must consider the distinct thresholds for i) habitat availability and ii) landscape (metahabitat) dynamics (Keymer et al., 2000).

Such natural patch and metapopulation dynamics can be found in river systems and their floodplains, which support a high diversity of habitat types on a small area, responsible for their extraordinary high biodiversity and conservation value (Richards et al., 2002). Particularly alpine rivers are very dynamic due to strong variations in discharge and sediment transport. The formation of different habitat types within the floodplain (Fig. 1.2) depends on the fluvial pattern and the given conditions, such as flow and sediment regime, lateral valley confinement and slope, as well as the regional plant pool (Hohensinner et al., 2018). Downstream the steep and narrow valleys typical for the headwaters of alpine rivers, widening of the river corridor and less steep slopes lead to a decrease in stream power and thus temporary deposition and relocation of sediments. So, braided or anabranching channel patterns develop, often dominating the entire floodplain with a large proportion of bare gravel and sand areas frequently affected by relocation processes (Tockner et al., 2003).

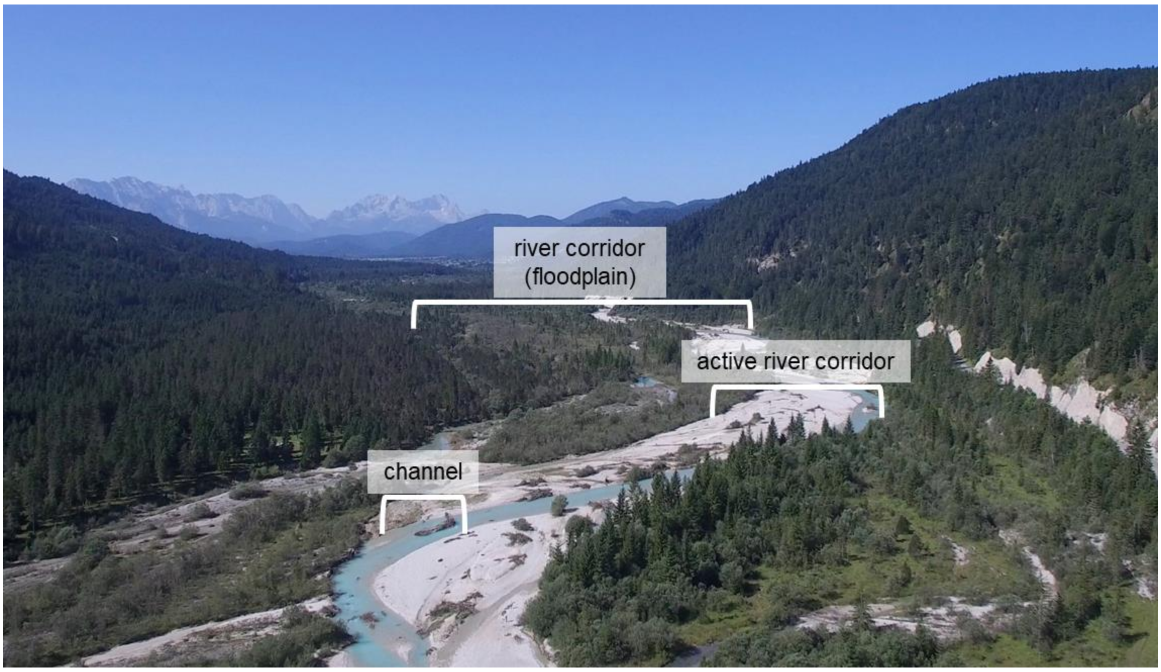


Figure 1.2 Riverscape units in alpine gravel-bed rivers (adapted from Belletti et al., 2015). 'Channel' means the water course and varies in its extent depending on discharge. The 'active river corridor' comprises the part of the floodplain that is affected by frequent floods and sediment turnover (every few years), so only early-successional vegetation can establish. The floodplain area or 'river corridor' additionally includes hard-wood forests and agricultural land only affected by extreme floods (HQ_{100}) (aerial photograph: River Isar near Wallgau, July 2017).

While floods of different magnitudes cause erosion or deposition of gravel and sand bars, and hinder the establishment of closed vegetation, successional processes on gravel terraces on a level above the frequent flood dynamic lead to sediment stabilization and a shift in vegetation types from pioneer states to willow scrub and forests (Edwards et al., 1999). Many species are restricted to certain successional stages, and each stage forms a distinct habitat type, leading to the strong patchiness of braided rivers. Especially early-successional plants, growing on sparsely vegetated gravel and sand bars, form metapopulations with pronounced colonization and extinction dynamics following the creation and erosion of gravel bars after floods and the gradual change of sites to unsuitable conditions due to succession (e.g. Stelter et al., 1997). Within a few years, a habitat patch will become unsuitable, making successful and fast colonization of new emerging patches within this period essential for population persistence (Charney and Record, 2016; Jäkäläniemi et al., 2005; Mestre et al., 2020). Successful colonization requires sufficient dispersal of propagules (hereafter 'seeds'), and many riparian plants produce seeds appropriate for wind dispersal to bridge the gap between patches. Still, most seeds are dispersed over only a few meters from the parent plant also in wind-dispersed species (Stöcklin and Bäumler, 1996). LDD of riparian plant species is possible via water transport downstream or through strong winds in both directions (Werth and Scheidegger, 2014; Wubs et al., 2016). Reaching suitable sites for germination via hydrochory requires flood events within the period of seed release, that dispose the seeds on safe sites, where germination and seedling establishment are possible (Merritt and Wohl, 2002). These events are rare and so is LDD, nonetheless it plays a crucial role for the connectivity in metapopulations, particularly in fragmented landscapes (Schurr et al., 2009).

Braided rivers and their early-successional riparian plant species are an ideal model system for studying the influence of metahabitat configuration on the persistence of populations (cf. Burkart, 2001), due to their patchy habitat distribution, high patch dynamics and the resulting metapopulations with frequent colonization and extinction processes. Assuming two-dimensionality of rivers and focusing on specialist species with a well definable habitat niche provides high potential for modelling approaches. Particularly investigations on the consequences of habitat fragmentation on metapopulations are not well understood, although of interest for several species groups living in patchy environments characterised by habitat destruction and disturbances, such as, for instance, agricultural or urban landscapes (Keymer et al., 2000). Moreover, the high biodiversity of braided riverscapes is of great conservation interest, since human impacts lead to a huge decrease in the respective riparian habitats, alteration of habitat dynamics (Fig. 1.3), and thus to a decline of many alpine river species, some of which are now critically endangered (Fig. 1.4).

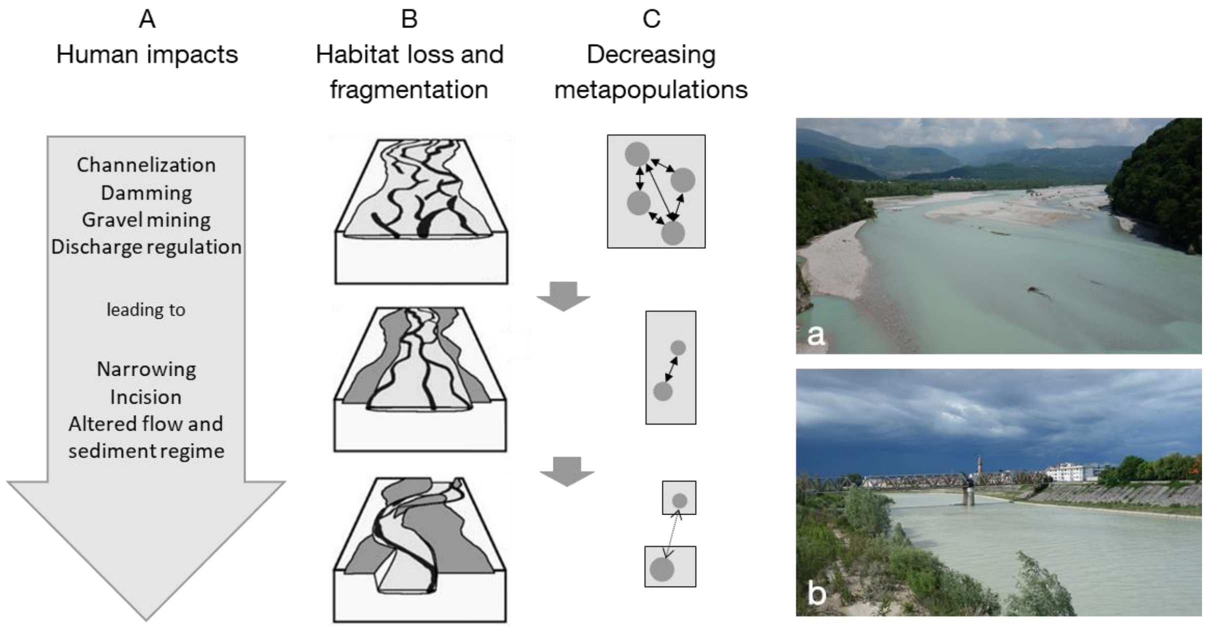


Figure 1.3 Consequences of human hydrogeomorphological impacts on Alpine rivers. Since the 19th century, engineering and land-use change have altered the appearance of most rivers (Grill et al., 2019). Particularly impacted are braided and anabranched rivers, which are the types with the greatest decrease in extent, i.e. on average about -70% in the Alps (Hohensinner et al., 2021; Woellner et al., 2022). For the Alpine region specific pressures are i) the land-use within the confined valleys and associated extensive flood protection measures, ii) high bed-load retention in the catchment area and iii) intensive use of hydropower (Muhar et al., 2019), leading to changes in river morphology and dynamics (A). Consequently, characteristic habitats got lost and fragmented (B), followed by the reduction and disruption of populations (C). The River Tagliamento (Italy) has still large braided reaches with almost natural dynamics (a), although it is channelized and decoupled from its floodplain in the lower reaches (b), like most major Alpine rivers.

Figure 1.4 In the Alps, many specialist species of gravel or sand bars in braided river reaches are under threat, e.g. the plants *Calamagrostis pseudophragmites* (a) and *Typha minima* (b), including the study species *Chondrilla chondrilloides* (c) and *Myricaria germanica* (d). Also some arthropods that prefer sparse vegetated gravel bars, largely lost their habitats through river engineering (e.g. Manderbach and Reich, 1996; Reich, 1991), for example *Bryodemella tuberculata* (e) and *Arctosa cinerea* (f).

State of restoration in Alpine rivers

Unfortunately, there is no consistent overview on river restoration projects for the Alpine countries (Muhar et al., 2019). Type, extent and success of measures along Alpine rivers are mostly described in case studies (e.g. Brousse et al., 2021; Muhar et al., 2007; Paillex et al., 2010; Scorpio et al., 2020), while some comprehensive studies on river restoration projects including all river types are available (e.g. Belletti et al., 2018; Kurth and Schirmer, 2014; Morandi et al., 2014; Muhar et al., 2016). Most projects focus on the hydromorphological state or the improvement of aquatic habitats, although multi-scale approaches are often recommended, addressing the entire floodplain system including terrestrial riparian habitats (Hohensinner et al., 2018; Kail and Wolter, 2011). 'Species conservation' is most frequently mentioned among the project objectives of Alpine river restorations (Muhar et al., 2019). Regarding the small-scale of most restorations, with only 15% of the projects contain river stretches of more than 5 km (>30% less than 1 km, Muhar et al., 2019), it is questionable, how metapopulation forming species could benefit from these measures in the long term (Fig. 1.5). Additionally, only few projects deal with restoring the longitudinal connectivity, or discharge and sediment dynamics (Muhar et al., 2019), which are crucial for species dispersal and the flood-induced formation of habitats.

Embankment removal and river-widening proofed to be successful in restoring the former channel morphology of braided rivers (Brousse et al., 2021; Devreux et al., 2022), with the highest potential in recreating gravel bars with pioneer habitats for early-successional plants (Woellner et al., 2022). However, for most endangered riparian plants a significant enhancement of the conservation state did not happen during the past decades of river restoration, and thus further efforts are required to recover fluvial biodiversity (Woellner et al., 2019).

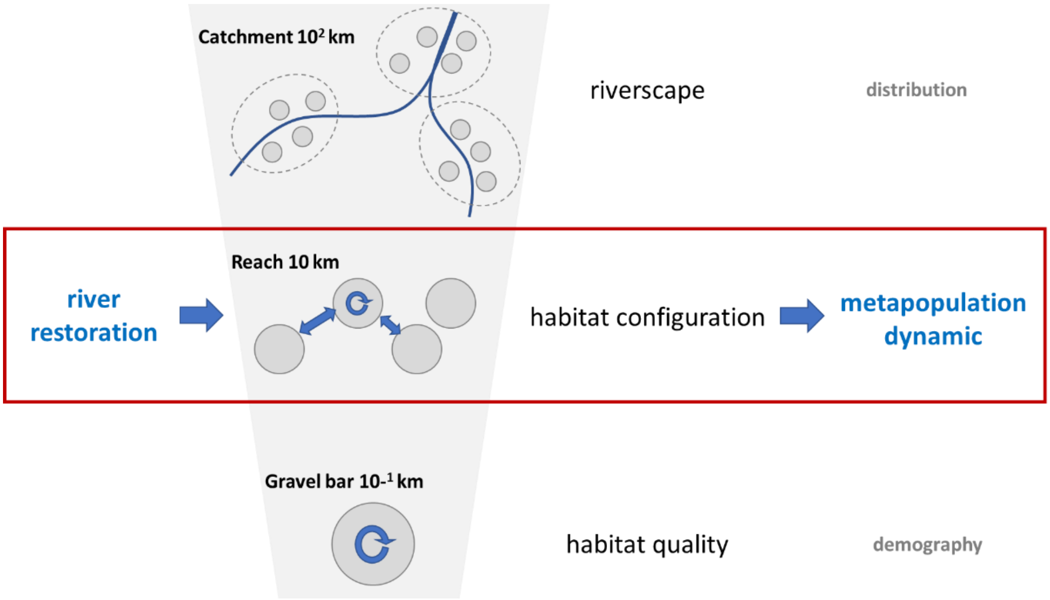


Figure 1.5 Spatial scales of research and restoration in river systems. Enhancing habitat quality at a local scale mostly supports demographic parameters of populations (e.g. fecundity). Most river restorations address the reach scale, aiming to restore habitats for target species. Still, many riverine species form metapopulations, so the actions must consider the configuration of habitat patches which often requires large-scale measures of several kilometres. Beyond, the natural river-specific processes and structures within the catchment determine the distribution range of the species and finally the alteration of river dynamics can limit the restoration success.

OUTLINE AND OBJECTIVES OF THE THESIS

The main objective of the thesis is to gain a better understanding of how habitat restoration and species conservation at Alpine rivers should act together to improve their success for maintaining biodiversity (Fig. 1.6). Here, a species-centred approach for evaluating spatial structures of habitats is used and applied to river restoration. Successful colonization as counterpart of local extinctions is crucial for population persistence particularly in dynamic systems (Jäkäläniemi et al., 2005; Reich, 1991). Though, it is often a limiting factor for population establishment after restoration (Brederveld et al., 2011) and a reason why many endangered species cannot sufficiently benefit from these measures. For restoration of dynamic systems, it is particularly challenging to increase not only the extent of suitable habitat but also to create the spatio-temporal arrangement of habitat patches ('metahabitat') that support metapopulations of target species. So far, it is rarely investigated which habitat configuration allows for successful colonization dynamics considering species-specific dispersal and recruitment in river systems.

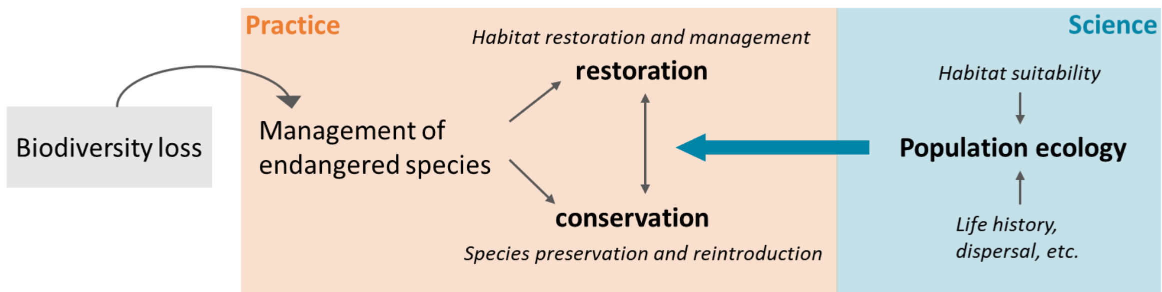


Figure 1.6 Overview of the interfaces of the scientific and applied topics addressed by the thesis. Biodiversity loss can be counteracted by management of endangered species. In practice, two approaches are used, i.e. restoration of ecosystems or management of remnant populations through preservation or reintroduction. Ideally, both approaches are combined, and restoration measures specifically address the recreation of habitats for endangered species, while suitable site conditions are restored before reintroductions are carried out. This cooperation can be supported by comprehensive scientific research on population ecology concerning both, habitat suitability analysis and species-specific life-cycle and dispersal characteristics.

The five publications of this thesis aim to answer the following questions:

I. What is the current state of habitat loss and restoration along Alpine rivers? (P1)
II. How can suitable habitats easily and standardized be identified? (P2)

III. What are the habitat requirements of the endangered riparian species? (P3, P6)

IV. How is the colonization process influenced by dispersal and establishment characteristics of the species? (P3, P4, P6)

V. What are the effects of habitat configuration on connectivity and colonization probability? (P5, P6)

VI. What should river restoration and species conservation do to sustainably support these specialist species?

The thesis focuses on two plant species with conservation relevance: *Chondrilla chondrilloides* and *Myricaria germanica.* They are early-successional species and form metapopulations on gravel bars along alpine rivers. Both rely on intact and frequent flow and sediment dynamics allowing for continuous early colonization. Today, the species are endangered and supported by several conservation programs (Sitzia et al., 2021; Woellner et al., 2020). They are characteristic for alpine braided rivers, and in case of *M. germanica* a suitable indicator for river restoration success (Sitzia et al., 2021). They co-occur along several river reaches and their population dynamics is driven by the same processes, but differ in some factors, such as dispersal ability and habitat niche. Therefore, the two species were studied using approaches at different spatio-temporal scales (Fig. 1.7) to address the above-mentioned questions.

Starting from the assessment of the habitat suitability and dispersal ability of two early-successional plants along Alpine rivers, the habitat configuration and connectivity in different river reaches (natural, degraded and restored) are analysed. Recent modelling approaches including habitat suitability, dispersal abilities as well as patch and river connectivity were developed for aquatic (Radinger and Wolter, 2015) or terrestrial animals (Saura and Pascual-Hortal, 2007), and applied to floodplain grasslands (Volk et al., 2018), or with coarse resolution for studying migration processes (Renton et al., 2012). However, they all do not match the certainties of wind-dispersed plant species on gravel bars. Thus, the thesis also presents an approach for connectivity modelling adapted for early-successional plants in dynamic systems (P5, P6). A concept on restoration and reintroduction under different scenarios of habitat patch fragmentation and river connectivity are derived from the results.

- **Publication 1** (P1) quantifies the loss and restoration success of pioneer habitats using analyses of historical maps and recent aerial images.

- **Publication 2** (P2) describes the novel methods of habitat assessment for analysing habitat suitability with UAVs.

- **Publication 3** (P3) summarizes ecology, threat and conservation of an endangered alpine river specialist *Chondrilla chondrilloides* in form of a monograph.

- **Publication 4** (P4) deals with the metapopulation structure of an endangered alpine river specialist and the colonization process of a relocated river site analysing population structure and gene flow.

- **Publication 5** (P5) presents new connectivity metrics that are specially developed for wind-dispersing plants in riverscapes, designed in a way, that habitat suitability models and extensions for further modelling can be easily implemented.

- **Publication 6** (P6) investigates habitat availability and connectivity of both study species by modelling habitat suitability and comparing habitat configuration and connectivity metrics (P5) of different river reaches (natural-degraded-restored) with dispersal characteristics.

The general discussion puts the findings together for resuming how restoration and conservation measures can be improved to support endangered, metapopulation-forming riparian species.

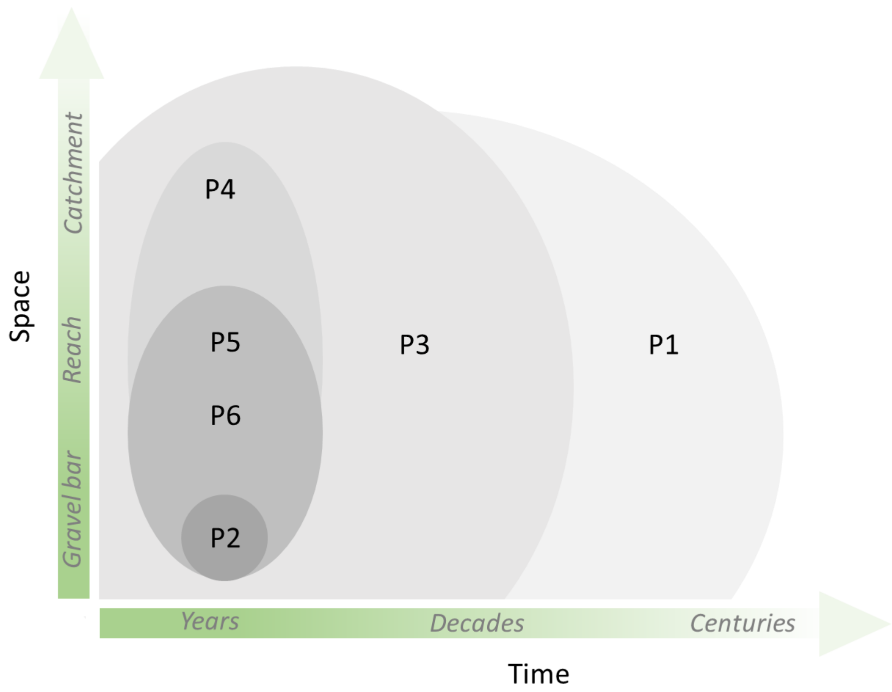


Figure 1.7 Overview of the spatio-temporal scales of the publications of the thesis (P1–P6). While P1 is dealing with the degradation of five German Alpine rivers from the mid of the 19th century until today, habitat assessment via drones (P2) was studied over two consecutive years in one alluvial fan of few hectare size. Publication 3 comprises the monograph of *Chondrilla chondrilloides* and includes germination experiments of a few weeks as well as the population decline among the distribution range during the last century. Studying the gene flow within the catchment of river Inn in *Myricaria germanica* populations (P4) based on population mapping and sampling within a few years. The investigation on connectivity (P5) and habitat availability (P6) was carried out along five contrasting reaches of river Isar including field mapping and drone data from 2017–2018.

METHODS

Study region and study sites

Data collection for the five publications was carried out within the Eastern Alps (Marazzi, 2004) at three rivers or streams in the northern study region (Friederlaine, Isar, Lech), one river in the central region (Flaz) and three ones in the southern region (Piave, Rio Alba, Tagliamento) (Fig. 2.1). These Alpine systems are gravel-dominated watercourses with prevailing limestone and dolomitic sediments. The average discharge corresponds to a typical snow- and glacier-melt regime with highest discharges between May and September. While rivers in the northern and central Alps show only one peak with highest discharge, rivers in the southern Alps have two peaks, due to increased precipitation in spring and autumn (Egger et al., 2019). High floods usually take place in summer (June–August) as consequences of heavy rain falls.

The study rivers differ in type, size and extent of human impacts, but all support populations of at least one of the study species, i.e. *C. chondrilloides* or *M. germanica*. An overview on the climatic, hydrological and ecological characteristics of the study sites 1–4 (cf. Fig. 2.1) is given as short profiles in Appendix 1, as they are either part of multiple publications or studied in detail within one publication. Study sites 5–8 were used for data collection referring to species characteristics (P3) and as natural references, but not for habitat or population modelling, and site descriptions are shown in the appendix of P3.

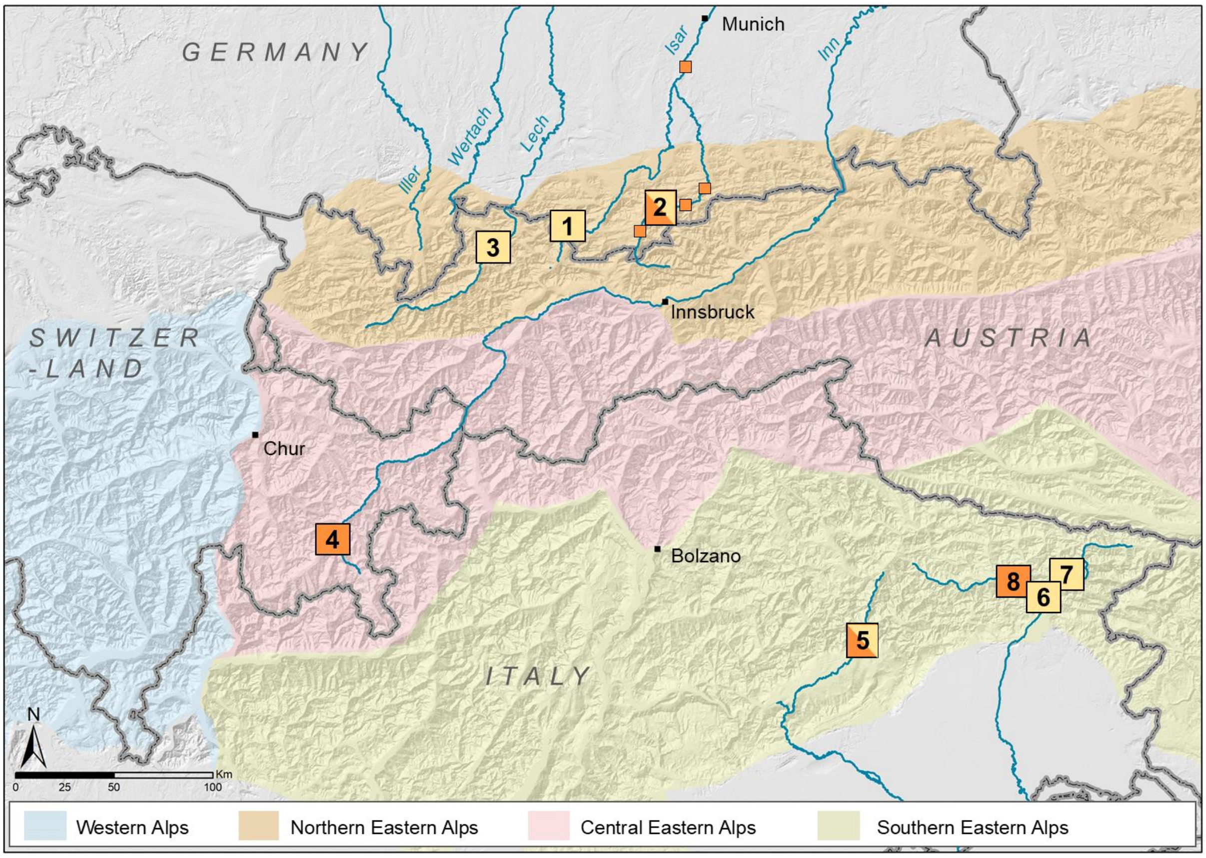


Figure 2.1 Location of the study sites with populations of *Chondrilla chondrilloides* (yellow) and *Myricaria germanica* (orange) along gravel rivers in the Alps: 1 Friedergries, 2 Isar, 3 Tyrolean Lech, 4 Flaz, 5 Piave, 6 Fella, 7 Rio Alba, 8 Tagliamento. Small orange squares represent the different study populations of *M. germanica* along the river Isar.

Study species

Both study species, *Chondrilla chondrilloides* and *Myricaria germanica*, are early-successional plants of alpine rivers. Thus, in several stages of their life cycle and ecophysiology they are adapted to the fast changing site conditions due to erosion and sedimentation during flood events. Further, natural patchiness and spatio-temporal variation in habitat availability result in a metapopulation structure of both species. They are very light-demanding during germination and seedling establishment, and poor competitors that are quickly overgrown for example by willow scrub. As they share similar habitats and rely on intact river dynamics, both species suffered from engineering measures along Alpine rivers during the past 200 years. They disappeared from most river reaches of their former distribution range and only a few large populations persist, corresponding to remnants of near-natural river reaches.

Chondrilla chondrilloides is a rosette forming hemicryptophyt of the Asteraceae (Fig. 2.2). A monographic description of the species is given in Woellner et al. (2022b) (P3). The size of adult plants varies between 5–28 cm in rosette diameter and 10–30 cm stalk height. The stalks, which are multibranched in the upper parts, produce up to 250 floral heads with 9–12 yellow linguate flowers per head. The plant is mostly insect-pollinated by hoverflies and bumblebees, and selfing is prevented by protandry. The seeds are beaked achenes with pappus and mainly wind-dispersed. Primary dispersal is assumed to reach a range of about 14 m (95% seed kernel), while longer distances can be covered by water dispersal or through strong-wind events.

Chondrilla chondrilloides is a character species of the pioneer community on calcareous scree along Alpine rivers, streams and alluvial fans. It underwent a strong decline within the entire distribution range which is naturally restricted to the Eastern Alps. Today, the species is almost extinct in the Northern and Central Eastern Alps, where a few small populations remain, while there are still larger populations in the Italian region 'Friuli'. It is listed on the national red lists of the Alpine countries as 'endangered' or even 'critically endangered'; also the IUCN lists the species as 'endangered'.

Figure 2.2 Habitus of an adult almost flowering individual of the gravel-river specialist *Chondrilla chondrilloides* (a) and a few weeks old seedling (b) (photos: Tyrolean Lech, July 2019).

Myricaria germanica is an erected nanophanerophyt of the Tamaricaceae (Fig. 2.3). A monographic description of the species is given by Sitzia et al. (2021). It can reach a height of 3 m and produces pinkish to white flowers aggregated in racemes, which are terminal at the current year shoots. The species is insect-pollinated but also capable of self-pollination. Capsules contain about 100 small, shafted seeds, that are well suited for wind or water dispersal (Sitzia et al., 2021). The average dispersal distance is about 30 m (Fink et al., 2017), but most seeds fall next to the mother plant. Longer dispersal distances of >10 km were reported (Sitzia et al., 2021), and most likely depend on strong winds or flooding. *Myricaria germanica* can resprout from roots or shoots after damage, and an asexual reproduction from plant parts that have been washed away is likely.

Myricaria germanica grows on sparsely vegetated gravel and sand bars along alpine and mountain rivers and is considered an indicator of braided gravel-bed rivers with natural dynamics. The species is also included in national red lists of many European countries, as only few larger populations remain along natural and semi-natural rivers like Durance (F), Isel (A) and Tagliamento (IT) (Sitzia et al., 2021). The IUCN lists the species as 'vulnerable'.

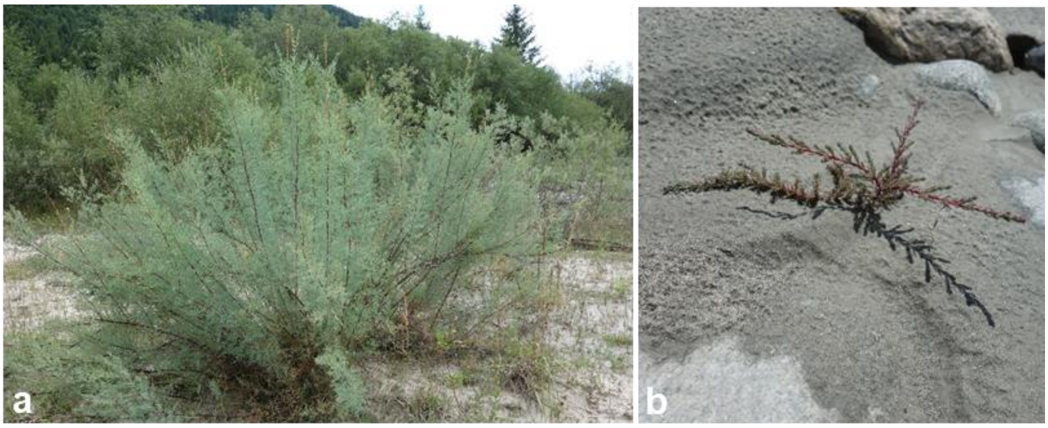


Figure 2.3 Habitus of an adult *Myricaria germanica* shrub (a) and a young plant (b), another specialist of gravel rivers in the Alps (photos: River Isar at Wallgau, August 2017).

Data sampling

<u>Aerial image analysis (gravel bar area)</u>

For assessing quantitative decline and restoration of gravel bars along Alpine rivers historical maps (mid-19th century) and aerial images from 1960–2015 were analysed (P1, Fig. 2.4). The study was carried out at five large rivers in Bavaria with a special focus on river Isar that has the highest conservation value and offers appropriate restoration sites for evaluation.

For each of the five rivers (Lech, Iller, Inn, Isar and Wertach) ten sites were chosen to quantify change in gravel bar area between the historic state (before 1900) and today (2009). Additionally, for analysing detailed changes in river corridor composition along river Isar three sites with different degrees of degradation were evaluated in three time steps, i.e. 1900–1960, 1960–1980 and 1980–2012. To assess areal gravel bar changes after restoration four sites at river Isar were investigated using different times series between 1987 and 2015 in 3–6 year intervals according to availability of aerial images and year of restoration measure. For all analyses habitat types within the river corridor were digitized as polygons by hand, i.e. water, bare gravel, pioneer vegetation, willow scrub, riparian forest and others.

UAV flights and imagery preparation

Geotagged nadir aerial images were acquired (P2, P3, P6) using a commercial Phantom 4pro and mavic2pro (both DJI) equipped with a standard camera. All flights were conducted at about mean water with mission planning using the MapPilot pro App (Fig. 2.4).

Flight height was 40 m above ground level, image overlap was set to 70%, flight speed varied from 2–5 m s^{-1} adjusted according to light conditions, keeping motion blur under 2 cm. The resulting images had a resolution of about 2 cm per pixel. The processing software AgiSoft MetaShape 1.8.2 was used to generate orthomosaics and generate digital elevation (DEM) and digital surface models (DSM) via the surface from motion approach, following the 'Best Practice Tutorial DJI Phantom 3 Professional' (see P2). Ground points were automatically identified by MetaShape ground point classification tool (Röder et al., 2017) with a maximum distance set to 0.1 m, angle set to 5° and cell size set to 5 m. Further processing and analysis was done using ArcGIS 10.7.1 and QGIS 3.10.10 respectively using the UTM 32 coordinate reference system. The river channel and active river corridor were manually digitized and applied to all raster data as mask, to exclude water areas and floodplain areas beyond the current river dynamics (P6).

Population surveys

The study sites were carefully searched for the study species by walking in zigzag-patterns across potential habitat sites. All plants were mapped via GPS (Garmin 66S) and life stages were recorded in three classes, i.e. young plants, flowering adults, and non-flowering adults. Juveniles and adults were distinguished based on their size: in *C. chondrilloides* individuals with a rosette diameter <5 cm were classified as 'young', while in *M. germanica* this was applied for individuals with a height ≤20 cm (P6). Further, morphological traits were recorded, for *C. chondrilloides* rosette diameter, stalk height and number of flower heads (details see P3), for *M. germanica* plant height and proportion of dead wood. In both species height was not measured directly, but estimated in steps of 5 cm (P3, P6).

Genetic sampling of *M. germanica* population along the river Flaz (Fig 2.1), 168 randomly selected plants (of 637) were sampled, taking about 5 g of small leafed branches per plant

(P4). Genetic data and samples from eleven potential source population in the catchment of river Inn were derived from an earlier genetic study.

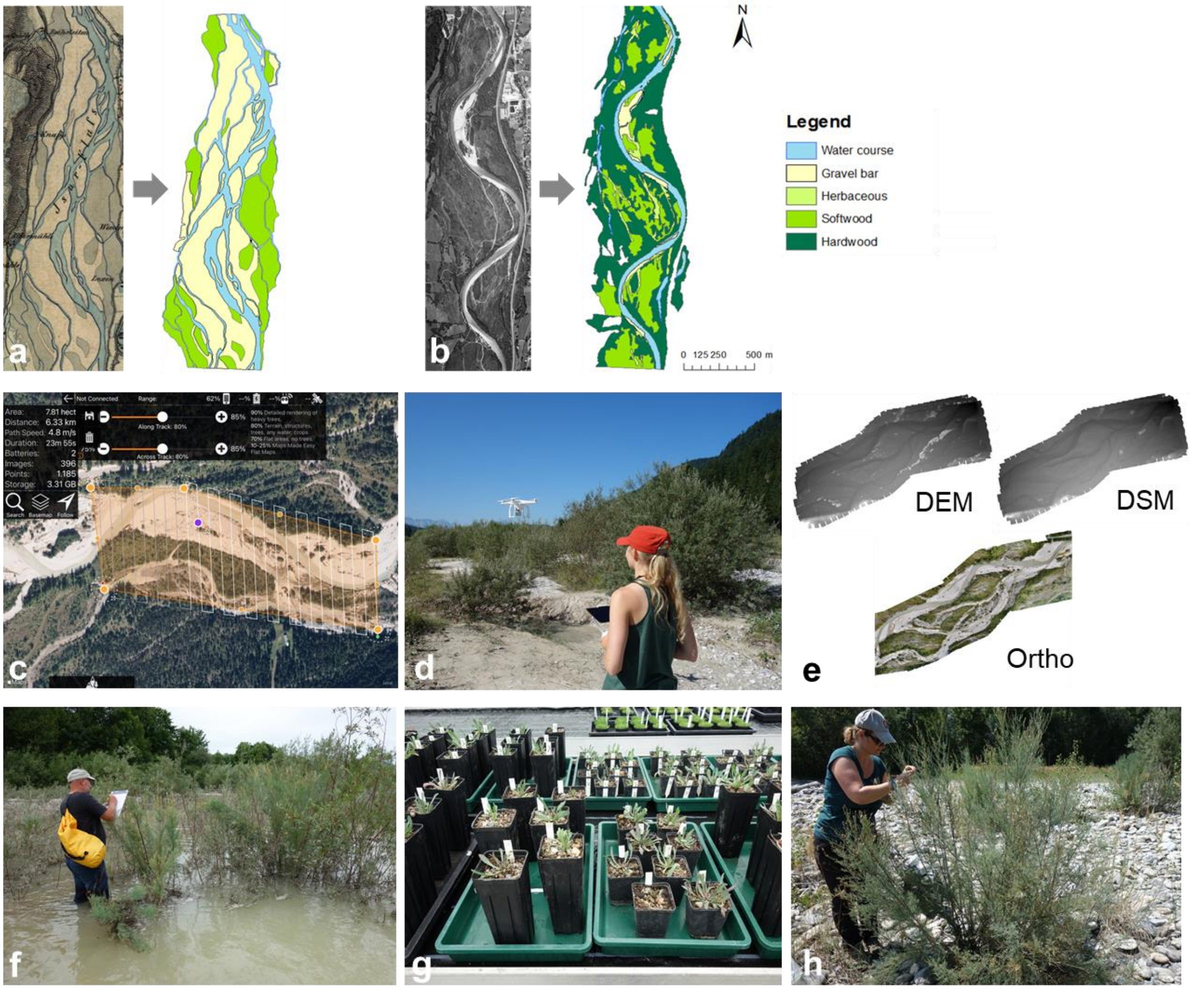


Figure 2.4 Overview on sampling methods of the thesis. For investigation on floodplain and gravel bar change, habitat types on historical maps (a) and aerial images (b) were digitized. The basis for habitat assessment were digital elevation models (DEM), digital surface models (DSM) and aerial images (orthos) (e) derived from drone flights (d), that were conducted automatically via mission planning in MapPilot Pro (c). Data on study species were collected in the field as population surveys (f) and genetic sampling (h), and for *Chondrilla chondrilloides* also with greenhouse experiments (g).

Data analysis

<u>Assessment of gravel bar area and historical time series</u>

The loss in gravel bar area along the five major rivers was calculated comparing the proportion of gravel bar area between the historic state and today for the respective sites. For the three sites at river Isar it was assessed to which extent gravel area got lost to either a loss in active river corridor area or to succession. Thus, the current area of the active river corridor was related to the historical area of the river corridor. Further, the proportion of gravel bar area and vegetated area were related to each other resulting in the *Gravel Index,* ranging from +1 (100% gravel area) to -1 (fully vegetated river corridor).

The same comparisons were applied to the restored sites, but with the pre-restoration state of active river corridor and gravel bar area as reference. Here, changes in gravel bar area after restoration were correlated to flood events that occurred within the respective time intervals, to investigate their potential contribution to the creation of gravel bars. The discharge of the floods was largely proportional to the maximum discharge of the period, so for intuitiveness the changes in gravel bar area were related to the maximum discharge of the respective flood. Except for the years 2000–2003 only one flood higher than the mean high water took place in every time period.

<u>Parameters for assessment of the habitat preferences</u>

Climatic conditions were assumed to be largely similar between the study reaches and not significantly influencing the habitat suitability on gravel bars. For early-successional and low-competitive species, light availability is crucial for germination and seedling establishment (Sitzia et al., 2021, P3), which is mostly driven by vegetation cover and height of the surrounding vegetation. Additionally, water availability controls successful recruitment of early colonizers (Stöcklin and Bäumler, 1996) that is influenced by the vicinity to the water table and sediment composition. Consequently, four habitat parameters were chosen that most likely have the greatest importance for site suitability, i.e. cover and height of vegetation, terrain height above water table and the proportion of sand. The datasets from the UAV flights were the basis for the assessment of these habitat parameters.

Vegetation cover and height mainly determine light availability on the gravel bars. High cover and large shady shrubs and trees may hamper germination and seedling development of the early-successional species and can also outcompete older life stages. Vegetation cover was determined using the Excessive Green index (Meyer and Neto, 2008). Its calculation based on the standard orthoimages, and thresholding was applied to differentiate between vegetation (1) and bare ground (0). Vegetation height was calculated from the difference between DSM and DEM and the overlay with the vegetation cover.

The **terrain height** of the gravel bars above mean water table is a measure for frequency and also intensity of flooding on the respective sites, which is highly relevant for the establishment of the study species (Gostner et al., 2017; Sitzia et al., 2021). Higher sites are less frequently flooded, usually older but depending on their age and water availability in many cases also more densely vegetated. Habitat niche of the pioneers are hypothesized to lie between a too high risk of erosion and too far advanced succession. The terrain height was calculated from the DEM. To get the height of the habitats in relation to the mean water table another raster dataset was created with the height of the mean water table, considering the slope of the river course. For that, a set of elevation points (20–50) per study segment was created covering the entire area of the river corridor and a TIN (triangular irregular network) was generated. The resulting water-table-raster was then subtracted from the DEM.

The **proportion of sand cover** on gravel bars has an influence on water holding capacity and also nutrient availability. *Myricaria germanica* is known to better establish on sandy or silty sites that later can be covered with gravel (Lener et al., 2013). Thus, older plants can be found on gravel although establishment took place, while sand and silt dominated the surface sediments. Proportion of sand was identified using supervised image classification in ArcGIS. A set of 20–30 training samples was created per study segment and sand, gravel and vegetated areas were identified automatically as 'interactive supervised classification'. Results were checked visually against the orthoimage for accuracy rate and where necessary training samples were improved.

Using these modelling variables and the population census data the 90% surface range envelope (SRE) was determined. Around each point (plant) a buffer circle (radius 1.5 m) was generated, in which the average value for each habitat variable was calculated. Habitat preferences were determined separately for young and adult plants, because suitable colonization habitat can be overestimated as rejuvenation niche often differs from adult niche (Luna and Moreno, 2010). Differences between young and adult plants in respect to habitat parameters were tested using permutation t-tests (perm.t.test, R package RVAideMemoire; Hervé, 2020).

<u>Habitat suitability model (HSM)</u>

For investigating habitat availability, areas with a high probability of occurrences of the species were determined using the same raw datasets from the UAV flights as predictors for the HSMs (Fig. 2.5). For modelling, all data were aggregated to a raster with 5-m resolution to account for the deviation of the GPS coordinates of the plant census. The HSMs based on a set of generalized boosted regression models (R package biomod2 version 3.5.1; Thuiller et al., 2021). The presence data were complemented with ten sets of randomly selected pseudo-absences within the active river corridor. Pseudo-absences were restricted to cells where the predictors variables lie outside the 95% surface range envelope of the young plants to avoid pseudo-absences in suitable but unoccupied sites, which can become frequent in dynamic, dispersal limited systems. Model tuning was done by combining the presence data of each species with a random set of the respective pseudo-absences. The model with the lowest root mean square error was applied to the respective training area; a random fraction of 70% of the data was used for training, and 30% for model evaluation. The resulting ten model sets for each species were evaluated and assessed by determining relative importance of the predictor variables, AUC and TSS. The model sets were then used to predict the probability for the occurrence of *M. germanica* and *C. chondrilloides* for all sections of river Isar. The cut-off thresholds were applied to the averaged models to obtain a binary raster with suitable habitats for both species. The model results were then validated against the census data of the respective species.

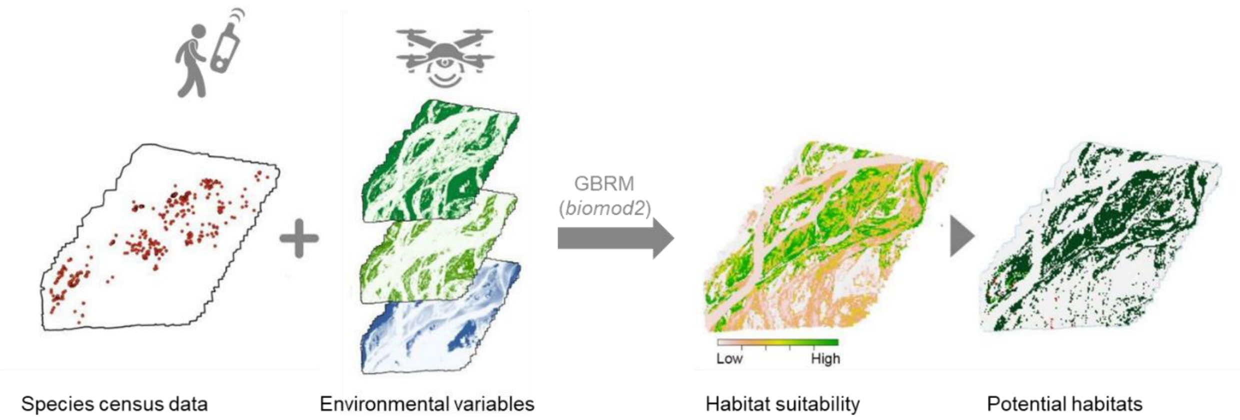


Figure 2.5 Workflow for the development of a habitat suitability model (HSM) for the study species to assess the potential habitats of a river reach. Species occurrences derived from field surveys and habitat variables (see 2.5) were the input for a set of gradient boosted regression models (GBRM; R package *biomod2*) to calculate the HSMs containing a probability of occurrence for each raster cell. After applying the respective probability thresholds, each study site was represented as binary raster with 5-m grid cells either assigned as suitable (1) or unsuitable (0) for the study species (changed after Schmid, 2019).

<u>Habitat configuration and connectivity</u>

Adjacent raster cells, identified as suitable, were grouped together to a *patch* and their size determined. Isolated patches with less than four cells were removed. Patches within the species dispersal distance of occupied patches were classified as *colonisable*. Suitable, occupied and colonisable patches were projected to the middle line of the active river corridor. River stretches between two projected suitable habitats with more than three times the species dispersal distance were identified as gaps, and their position and length were determined.

The colonization probability between patches was defined as a function of the patch distance, area and shape and the dispersal kernel of the respective species, irrespective of the actual occupancy of the patches. A set of spatially explicit metrics for wind-dispersed plant species was developed to evaluate the probability of colonization: *Effective Distance, Effective Connections, Number of Connections* and *Connection Capacity* (P5). It is assumed, that every suitable cell could host parents that disperse seeds to surrounding suitable patches considering the decrease in seed density, reflected by the species-specific dispersal kernel function. A patch was considered to be connected to another one, if at least two cells could exchange seeds due to their distance within the dispersal kernel. The strength of a connection between two patches grows with patch size and interface area, and decreases with the distance between the patches (Fig. 2.6).

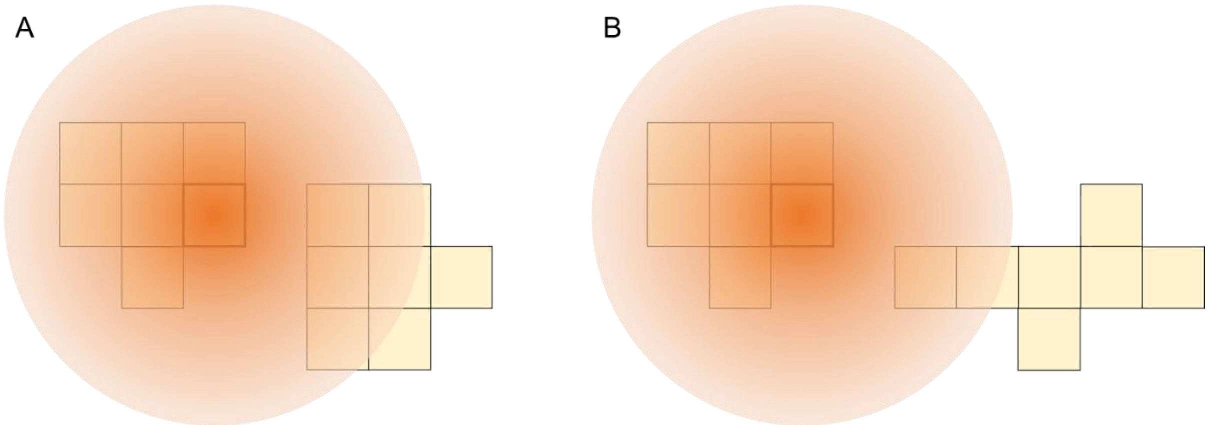


Figure 2.6 Effect of the patch shape on the interface between patches and therefore the potential exchange of seeds and connectivity between patches used for modelling habitat and population dynamics of specialist plants in gravel rivers. In situation A, the number of cells potentially receiving seeds of the right-handed patch are threefold compared to situation B, where small interface lead to a weaker connectivity of both patches, though they have the same size. Connectivity of the patches is calculated from the sum of seeds every cell can receive.

As the amount of seeds a cell can potentially receive is given in relative proportions following the dispersal kernel, the sum of seeds a patch receive can be translated backwards into a virtual distance, the *Effective Distance*, between patches. This can be directly compared to the dispersal distance of the species: colonization is improbable if the *Effective Distance* exceeds the maximum dispersal distance of the species.

Effective Connections, a measure for the strength of patch connections, is the weighted connection between patches, based on the sum of seeds a patch can receive per connection. Further, the *Connection Capacity* gives the ratio between the strength of connections to the

Number of Connections, reflecting the colonization probability per patch. The connectivity of river reaches can be estimated via calculating the means of the single index values.

Dispersal distances

It is distinguished between 'regular' short-distance dispersal (SDD) and long-distance dispersal (LDD). SDD means the distance the seeds fall down from the parent plant under average wind conditions. For *M. germanica* the dispersal kernel was adopted from a seed trapping experiment (Fink et al., 2017), for *C. chondrilloides* the kernel was determined accordingly using glue traps (P3). Additionally, the distances between juveniles and the nearest parent plant were included, to get an estimation about the 'realized' dispersal distance (Effective dispersal distance, EDD) and potential colonization via LDD (P3, P6). Calculations were done as nearest-neighbour analyses in ArcGIS.

The seed transport via the water flow under normal discharge conditions was not considered, because for successful establishment, seeds must reach higher gravel terraces that are not affected by annual floods. In contrast, large floods, that are also able to relocate gravel bars, can deposit seeds on these sites together with fresh sediments, forming suitable conditions for germination and seedling establishment. Floods also allow for the transport of eroded plants or in case of *M. germanica* of small branches and thus vegetative spread is possible. Together with storms, such flood events enable propagule dispersal over long distances up to >100 km (Nathan et al., 2008). LDD is much rarer than SDD and harder to predict, and therefore it was not included in the calculation of the dispersal kernel used for the estimation of the colonization probability. It must be considered, that despite their rarity, LDD events can have a decisive influence in the colonization of distant or new habitats and thus metapopulations dynamics (Bohrer et al., 2005; Johst et al., 2002).

Establishment-related plant traits

Beside the dispersal distance, amount of seed production ('propagule pressure'), germination rate, seedling growth and survival influence the colonization success in plant species (Stöcklin and Bäumler, 1996). For *M. germanica* information on recruitment-related traits are available (Lener et al., 2013, Sitzia et al., 2021), while for *C. chondrilloides* amount of seeds per plant, germination rates, and seedling growth were described within the monograph (P3), which provides details on the conducted experiments.

Genetic analysis

Genetic analyses were performed for 22 microsatellite loci following the protocol of Werth and Scheidegger (2011) using about 15 mg plant material (P4). Populations were tested for differentiation and sources of variations with a hierarchical *Analysis of Molecular Variance* (AMOVA), and pairwise F_{ST}-values were used for generating a principal coordinate analysis. For testing on genetic structuring considering population spatial distribution and number of gene pools (clusters) a Bayesian analysis was performed with ‘tess3r’ in R.

Accounting for the morphological differences of the occupied habitats, the population along river Flaz was divided into two subpopulations: i) same-aged and old plants along the artificial shoreline and ii) age-mixed plants on the gravel bars within the dynamic zone of the river. The entire Flaz population as well as the subpopulations separately were checked for differences in genetic diversity, distance to other populations and clustering (P4).

SUMMARY OF PUBLICATIONS

Publication 1: Spatio-temporal patterns in degradation and restoration of gravel bars along Alpine rivers

Woellner, R., Wagner, T. C., Crabot, J., Kollmann, J. (2022) Spatio-temporal patterns in degradation and restoration of gravel bars along Alpine rivers. *River Research and Applications, 38,* 738–756, doi: 10.1002/rra.3933

Author contributions

RW, TCW and JK designed the study. JC digitized aerial images and **RW**, TCW and JC analysed the data. **RW** and JC wrote the draft, TCW and JK corrected the manuscript.

Summary

The first article investigates the decline and restoration of gravel bars along Alpine rivers in Germany. While mechanisms of river degradation are frequently described in literature, analyses on the quantitative loss of gravel bars and the success of restoration measures in recreating them are rare. Over the past two centuries modification of Alpine rivers due to flood protection, land reclamation and hydro engineering changed river morphology radically. Braided reaches were channelized, floodplain area significantly reduced and gravel bars, as pioneer habitats, got lost. In this study, the historical and present state of 50 river reaches along five Bavarian rivers were compared and a loss in gravel bar area of >90% could be verified. A detailed view on the structural changes of the river corridor at three reaches along river Isar with different degrees of degradation showed that the impacts entailed a significant reduce in active corridor area parallel to the decline in gravel bars, mainly during the first half of the 20th century. Its more recent decrease is driven by succession on the remaining open sites due to ongoing alteration in discharge and sediment dynamics. Restoration projects along river Isar could rarely improve the proportion of gravel bars within the active river corridor of the respective site even 20 years after implementation. Size of the measure and high floods influence the restoration outcome; only at the largest restoration site the active river corridor has widened and gravel bar area increased in a significant extent. Though, affected discharge and sediment regime will further support succession and more extensive restoration measures are required for enhance biodiversity and adaption of Alpine rivers to climate change.

Publication 2: Saving species, time and money: Application of unmanned aerial vehicles (UAV) for monitoring of an endangered alpine river specialist in a small nature reserve

Woellner, R., Wagner, T. C. (2019) Saving species, time and money: Application of unmanned aerial vehicles (UAV) for monitoring of an endangered alpine river specialist in a small nature reserve. *Biological Conservation*, 233, 162-175. doi: 10.1016/j.biocon.2019.02.037

Author contributions

RW and TCW developed the study design. **RW** conducted the population census and **RW** and TCW perform the drone flights. TCW prepared and analysed the aerial image data, **RW** digitized habitats and deadwood. **RW** and TCW wrote the manuscript.

Summary

The article introduces a cost-effective and easy applicable method for a standardized evaluation of relevant parameters defining the habitat niche of the study species. The background is that conventional aerial images have a too coarse resolution in time and space for the naturally fast changing and small-scale habitat mosaic along alpine rivers. The method described in this article is an important part of the studies belonging to the thesis.

With the case study of the *Chondrilla chondrilloides* population in the Friedergries three habitat parameters were elaborated that determine the occurrence of the species: vegetation cover, vegetation height and terrain height. Additionally, dynamics of the stream channel, bedload transition and consequently the habitat change and extinction risk of the population could be calculated from the orthoimages made by a commercial UAV. Most *C. chondrilloides* plants grow on sites with pioneer vegetation with a coverage of 1–20%, height of 0.2–0.5 m and an average terrain height (above water table) of 2.1 m. Within one year significant bedload relocation was observed, with incision in the upper part of the alluvial fan and deposition 100–200 m downstream. The bedload transport and relocation of the stream channel resulted in a great loss of terraces with pioneer vegetation and thus a loss of 25% of *C. chondrilloides* habitats. Therefore, such constrained and small populations are prone to extinction due to heavy rainfall events, must be monitored very frequently and further conservation measures, like assisted colonization to other sites are crucial for preserving the species in the long-term.

Publication 3: Biological Flora of Central Europe: *Chondrilla chondrilloides* (Ard.) H. Karst

Woellner, R., Bräuchler, C., Kollmann, J., Wagner, T. C. (2022) Biological Flora of Central Europe: *Chondrilla chondrilloides* (Ard.) H. Karst. *Perspectives in Plant Ecology, Evolution and Systematics*, 54, 1-20. doi: 10.1016/j.ppees.2021.125657

Author contributions

TCW, CB and **RW** conducted field work, CB contributed genetic analyses of the species. **RW**, TCW and JK developed the concept, TCW and **RW** evaluated the data and prepared a first draft, JK and CB corrected the manuscript.

Summary

This publication summarizes all available information on the morphology, ecology and taxonomy on *Chondrilla chondrilloides* with special focus on the current population distribution, habitat requirements, seed germination and dispersal. The presented data serves as an important base for developing conservation strategies for the species as it is critically endangered in all Alpine countries and rarely considered in recent management planning.

The habitat and rejuvenation niche of the species is narrow and comprises sparsely vegetated gravel areas with higher elevation above the water table (older terraces) with an average age of 14 years. Population establishment needs relatively stable and flood-protected sites. With seeds traps a small dispersal distance of only 14 m was found that is also reflected by the nearest neighbour distance of juveniles to flowering adults, indicating a low colonization potential of new gravel bars.

The distribution range of *C. chondrilloides* is separated into two parts, one in the northern Alps and one in the southern Alps. While in the southern region plants are taller and large populations occur along several rivers and alluvial fans, in the northern region only a few populations remain, mostly isolated and with a higher risk of extinction. This pattern reflects the extent of river degradation within the Alps, where in the south floodplains are less affected by hydraulic engineering and population decline is far lower than in the north. There, conservation and restoration measures are necessary for the species long-term persistence. We describe successful *ex-situ* cultivation and reintroduction trials that demonstrate useful management options.

Publication 4: Gene flow in a highly dynamic habitat and a single founder event: Proof from a plant population on a relocated river site

Woellner, R., Scheidegger, C., Fink, S. (2021) Gene flow in a highly dynamic habitat and a single founder event: Proof from a plant population on a relocated river site. *Global Ecology and Conservation*, 28, 1-12. doi: 10.1016/j.gecco.2021.e01686

Author contributions

SF and CS developed the study design, **RW** and SF conducted field work, genetic sampling and lab work, **RW** analysed the data, **RW** and SF prepared a first draft, CS and SF corrected the manuscript.

Summary

This study took the opportunity to investigate the colonization of a river section that has been completely rebuilt. The river Flaz is located within the Inn catchment in the region Engadin (Switzerland), where a large metapopulation of *Myricaria germanica* occurs. A 3.6 km long section was relocated for reasons of flood protection but considering ecological aspects, particularly the development of gravel bars, that are potential habitats of the species. Fourteen years after relocation, we found a large population (>600 plants) of *M. germanica* and tried to trace the source of the new population and the colonization process. We mapped all individuals with their age classes and used microsatellite markers for the assessment of genetic diversity and relatedness to potential source populations within the catchment.

The population structure, with old and same-aged plants along the shoreline and young plants restricted to the dynamic gravel bars, indicates two distinct colonization processes. A first colonization event took place after a flood, when the embanked shoreline was still unvegetated and *M. germanica* could establish between the construction rocks. The close genetic relationship to the plants growing on the dynamics gravel bars reveal a secondary colonization of the frequently new created open sites with seeds from the shoreline plants. Their source cannot be attributed to one particular population upstream, but several founder individuals leading to a differentiated and diverse new population along river Flaz. We conclude that flood events within a river continuum are necessary to ensure colonization of new habitats by multiple sources via long-distance dispersal. Also, population parts outside regular river dynamics can act as sources for rejuvenation habitats with shorter turnover times.

Publication 5: A new set of metrics to quantify the colonization potential of riverscapes by wind-dispersed plant species

Wagner, T. C., **Woellner, R.** (2023) A new set of metrics to quantify the colonization potential of riverscapes by wind-dispersed plant species. *Preprint, Research Square*, doi: 10.21203/rs.3.rs-2388009/v1

Author contributions

Both authors contributed equally to the paper. TCW and **RW** developed the concept, analysed the data, and wrote the manuscript. TCW implemented the R package.

Summary

The persistence of populations in patchy and dynamic environments, such as rivers, bases on successful colonization processes. For example, early-successional plant species, mainly wind-dispersers but with limited dispersal distances are particularly vulnerable to changes in the spatial configuration of habitats and fragmentation of the riverscape and today multi-threaten by river engineering. The study focus on assessing the colonization probability and connectivity of riparian plants within river reaches as base for conservation and river restoration planning. Several recent connectivity measures for river networks focus on aquatic components, while connectivity metrics for terrestrial ecosystems have been developed for animals, and the particularities of the dispersal of plant species within riverscapes are not considered.

The study presents a set of cell-based, spatially explicit measures for quantifying the colonization potential of wind-dispersed plants in riverscapes. The metrics are tested for two characteristic and endangered plant species at three different braided river reaches, which differ in habitat configuration and connectivity. The metrics consider shape and size of the habitat patches, along with the dispersal characteristics of the respective species. They provide a linear, balanced, and realistic representation of the colonization potential at the cell, patch, and riverscape levels. The results are comparable between different riverscapes and species, and can easily be extended and used for further modelling.

With these properties, the riparian connectivity metrics provide valuable tools for the planning and evaluation of conservation, restoration, and reintroduction measures and close the gap between simple habitat availability analyses and large-scale or animal-tailored connectivity indices.

Publication 6: A habitat is not enough - Dispersal limitation rather than habitat loss is responsible for the decline of Alpine river specialist plants

Wagner, T. C. and **Woellner R.** (in prep.)

Author contributions

TCW and **RW** developed the study design, collected the data and prepared model inputs. TCW conducted model runs and statistical analysis. TCW and **RW** interpreted the data, **RW** prepared the manuscript draft, TCW and **RW** developed the manuscript for submission.

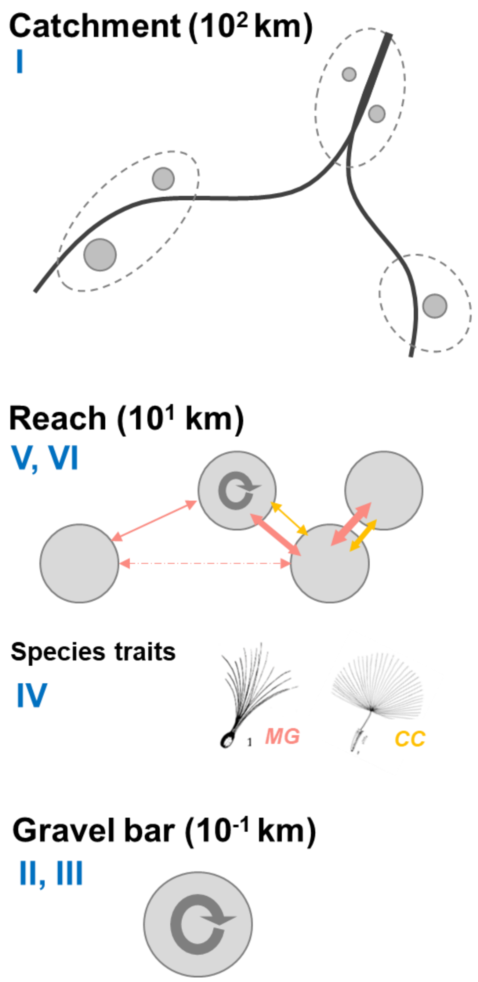
Summary

This manuscript investigates the consequences of altered spatial habitat configurations on the colonization probability of the two study species *Chondrilla chondrilloides* and *Myricaria germanica.* The habitat niche, dispersal abilities, patch configuration and connectivity are compared between the species and between differently degraded river reaches along river Isar. The habitat niche was determined using habitat suitability modelling based on analysis of UAV imagery. Dispersal kernels from previous studies were considered in the calculation of colonization probability and patch connectivity of the suitable habitats.

Both study species react in a different way on varying habitat configurations. With a shorter dispersal distance and narrower habitat niche, *C. chondrilloides* is more sensitive to habitat fragmentation in terms of larger patch distances than *M. germanica*. The investigations on the habitat configuration showed in general less habitat amount and patch distances far above the dispersal distances of the species. Although at near-natural sites with large gravel areas and available habitat, populations have become extinct, most probably due to large gaps in the patch network. However, along degraded reaches half the habitat is available and patch connectivity values reach only one third compared to near-natural sites, also for *M. germanica*, resulting most probably in an extinction debt of the remaining population there. For successful colonization processes patch distances should lie within the species' short dispersal distance, as long-distance dispersal is rare and hampered through river management. The species-specific differences in habitat niche and colonization probability are of high conservation concern, as restorations and reintroductions can only be successful in supporting endangered riparian species when meeting their requirements at the reach scale.

GENERAL DISCUSSION

Today, many efforts are made to reduce the negative impacts of human activities on aquatic and associated terrestrial communities and to preserve or restore the naturally high biodiversity of Alpine river ecosystems (Habersack and Piégay, 2007). River restoration mainly aims to facilitate natural processes, structures and ecosystem functions, sometimes without considering requirements of particular species with almost no benefit for endangered specialists. In dynamic environments, there are particular challenges in assessing habitat suitability, due to patch dynamics on varying spatio-temporal scales. This study could identify effects of degradation and restoration on the habitat configurations and the colonization probability (Fig. 3.1). The results can support conservation and restoration come closer together and optimize their measures for saving threatened riparian specialists on the long-term.



I) About 80% of gravel bar area got lost during the last century. Restorations were only partly successful in establishing gravel bars (best case: +5% to pre-restoration state). Concomitants are reduces in ARC and lower GI. (P1)

II) UAV imigary proofed to be a easy, cheap and replicable method to assess the main habitat parameters for the study species. HSM should use presence of young plants as input, due to the variances between regeneration and adult niche. (P2)

III) SREs of the study species are overlapping, but *C. chondrilloides* is more restrictive and prefers higher terraces. As expected, both require sparsely vegetated gravel bars, with low vegetation. (P3,6)

IV) Colonization potential varies between species, regarding shorter dispersal distance and lower seed production in *C. chondrilloides*. Germination and seedling growth is high for both and probably not the limiting factor for colonization success. (P3,4,6)

V) River degradation is accompanied by lower proportions of suitable habitat, smaller patches and higher distances between patches. Configuration is even worse for *C. chondrilloides* and more detrimental because of a lower colonization potential. Connectivity is low under degradation, resulting in low colonization probabilities. Restoration only slightly improved habitat situation for the species. (P5,6)

VI) Habitat loss is accompanied by a fragmentation of the patch network, hampering population recovery and causes extinction debts. Focus must lie on restoration of nearby suitable patches or river dynamics that allows for stepping-stones and LDD. The many spatio-temporal dimensions are best considered by a metahabitat concept for each species and river system.

Figure 3.1 Synthesis of the main results of the thesis related to different spatial scales (cf. Fig. 1.5). Roman numbers refer to the study questions (see *Outline and objectives of the thesis*). Losses in gravel bar area on the catchment scale are linked decrease in *Active River Corridor* (ARC) area and *Gravel Index* (GI), and thus to reduced habitat availability for the study species *Chondrilla chondrilloides* (CC) and *Myricaria germanica* (MG). Degradation led to less suitable habitat within river reaches and an unfavourable configuration with smaller patches and larger distances among them. This results in low connectivity, particularly for *C. chondrilloides* (yellow arrows) with short dispersal distances and thus lower potential seed exchange between patches than *M. germanica* (pink arrows). Further, in the thesis methods were approved to assess habitat suitability on the scale of gravel bars, which is essential in patchy environments with high habitat turnover.

Habitat suitability of the study species

Using aerial imagery for habitat assessment

With the analysis of historical maps, historical and recent aerial photographs the change in gravel bar area, vegetation units and extension of the (active) river corridor were delineated for major rivers in Bavaria (P1). Digitizing river morphology and riparian vegetation structures to assess long-term temporal changes in fluvial system is a widely used method (Rusnák et al., 2022), but has its limitations in spatio-temporal resolution. Aerial photographs from official flights conducted about every three years or mostly coarse satellite data cannot provide the required resolution for the small-scale and frequent turnover of riparian pioneer habitats.

Thus, P2 demonstrates the application of UAV imagery to get high-resolution data appropriate for habitat suitability modelling at a reach scale with relevance for local populations. Including cover and height of vegetation, terrain height above the water table and proportion of sand areas, the habitat niches of *C. chondrilloides* and *M. germanica* could be adequately defined (P3 and P6). The parameters have been identified as appropriate model input for later habitat suitability modelling for both study species leading to a high accuracy in habitat prediction of >90% (P6). Apart from these four variables, other factors on plant growth are soil moisture, that is most critical for germination and plant establishment on dry or rocky sites (Questad et al., 2014) and nutrient availability were neglected, because of an assumed minor relevance for the study species, a more or less homogenous distribution within habitat types, and a strong correlation to the analysed variables.

It is suggested that UAV images and the derived environmental parameters are appropriate for determining habitat requirements of several early-successional species and can be recommended to monitor habitat turnover adjusted to the occurrence of catastrophic events or restoration actions (P2).

<u>Habitat preferences vary between study species</u>

The HSM and SRE results (P3, P5) could quantify former descriptions of the habitat of *M. germanica* and *C. chondrilloides*. Both study species prefer sparsely vegetated sites on gravel and sand in the active zone of alpine rivers (Leuschner and Ellenberg, 2017; Sitzia et al., 2021). The habitat requirements of both study species are similar and overlapping, but *C. chondrilloides* requires smaller amplitudes (A2, Fig. A2.1) within the environmental space and thus has a more restricted habitat niche (P3, P6).

There were significant differences between the habitat preferences of juveniles and adults in *M. germanica* (P6). Young plants showed a smaller niche and occurred more frequently on sites with less vegetation cover and at lower height above the river, and with higher proportions of sand. For the species, large cohorts of seedlings appearing on sandy sites near the water table were reported (Kudrnovsky, 2013). This can be attributed to i) a general higher probability of reaching these sites, due to larger dispersal distances, ii) more favourable germination conditions with sufficient moisture and light provided there, and iii) occasionally colonization after moderate floods, when seeds are deposited with finesediments. In *C. chondrilloides* differences between the adult and the rejuvenation niche were smaller, but with a similar tendency of young plants occurring on sparser vegetated sites. The very similar site conditions of young and adults are presumably due to i) the limited dispersal of the species leading to short distances between juveniles and the parent and ii) lower probability of hydrochory, because the main occurrences are on higher terraces farther away from the water course. In cases, where the adult niche differs from the regeneration niche, as shown for the study species, the HSM should be based on the presence data of seedlings and saplings. Otherwise, the model can result in identification of suitable habitat, that actually does not meet the requirements of early-life stages and are thus not available for colonization (cf. Guerra-Coss et al., 2021; Poorter, 2007).

The higher terraces, with the main occurrence of the *C. chondrilloides*, exist on average for more than 14 years, characterized by the development of a biocrust (P3). Here, occurrences of seedlings of *C. chondrilloides* are often associated with large stones (Harzer, 2016), that thus seems to provide safe microsites, where moisture from rainwater can be stored, supporting successful germination and seedling survival (Stöcklin and Bäumler, 1996). This explains the weak sensitivity of the species to sand cover, but implicates the need for refining the variables in assessing *C. chondrilloides* rejuvenation habitat, to avoid an overestimation in modelling the habitat suitability of the species.

<u>Habitat amount varies between river reaches</u>

The HSM resulted in very variable proportions of suitable habitat area between sites and species. Through the narrower habitat niche, considerably less habitat was identified for *C. chondrilloides* ranging from 6–15%, in contrast to *M. germanica* with 30–70%. The proportion of suitable habitat for *M. germanica* corresponds well to the *Gravel Index*, but a significant relationship has to be tested with more study sites (A2, Fig. A2.2). However, near-natural sites (with a higher *Gravel Index*) provide a more suitable habitat for the species, but this trend is not pronounced for *C. chondrilloides*. The fact that the amount of suitable habitat for *C. chondrilloides* does not appear to be related to the degree of dynamics within the river corridor underscores the special conditions necessary for the development of suitable habitat for *C. chondrilloides*. The combination of a lower vegetation cover but a greater terrain height preferred by the species is rare, as succession is mostly reversed by floods, which are more common at lower sites that are more frequently affected by habitat turnover (Räpple et al., 2017).

Hence, suitable habitat for *C. chondrilloides* is likely to be naturally rarer than habitats of *M. germanica*. The near-natural reference sites (rivers Piave and Lech), which host large populations of *C. chondrilloides*, provide 15–20% suitable habitat, that appears in large continuous patches (Schmid, 2019), while for *M. germanica* 60–70% was identified as suitable at the reference site. River degradation led to a reduction of about 50–70% in suitable habitat area for both species. The decreased habitat amount might result in the species falling below the fragmentation threshold, from which the configuration of patches gets significant influence on population persistence (Villard and Metzger, 2014). This threshold is reported to lie at about 30% remaining habitat depending on the species under consideration (Parker and Mac Nally, 2002; Püttker et al., 2020; Villard and Metzger, 2014). The decrease in gravel bar area alone was found to be 80–100% in degraded and also 65% in the near-natural sites (P1), and loss in habitat will probably even exceed these values at the respective reaches. Thus, it can be assumed that species with more restricted habitat requirements, like *C. chondrilloides,* earlier reach the threshold, below which colonization processes are hampered, than more generalistic species. Although *M. germanica* is an alpine river specialist, it is mainly significantly impacted under stronger river degradation and in general still more widespread than *C. chondrilloides*.

The loss of gravel bars and thus the decline in habitat area turned out to be related to a shift from multi-channel to single-channel and oscillating channel forms and a reduction of the active river corridor (P1), in accordance to several studies on morphological changes in gravel-bed rivers (e.g. Comiti et al., 2011; Heckmann et al., 2017; Juszczyk et al., 2020; Surian et al., 2015; Ziliani and Surian, 2016). The results can be transferred to most European Alpine rivers, that lost their braided reaches in average to 70% of their former length (Gurnell et al., 2009; Hohensinner et al., 2021).

The decrease is less in the countries of the southern Alps, i.e. Italy (-35%) and France (-40%). The higher proportion of braided river reaches results in higher habitat availability than in the northern and central Alps and reason for larger populations of the target species in the South (Hohensinner et al., 2021; Sitzia et al., 2021; P3). However, while *C. chondrilloides* almost completely vanished from the Northern and Central Alps (P3), *M. germanica* is still occurring in large populations along the remaining gravel bar providing river reaches (Müller et al., 2019). As suitable habitat for *C. chondrilloides* is still available, although in smaller extents, fragmentation in combination with dispersal limitation are probably the drivers for the decline here and require more attention (P3, P6).

Dispersal ability and colonization potential

Dispersal kernel and distances

There are pronounced differences in dispersal distances between the study species mostly caused by their different life forms. *Chondrilla chondrilloides* has a SDD of only 14 m (P3), while *M. germanica* achieves about 30 m (Fink et al. 2017), mainly caused by its smaller seed size and greater release height (cf. Thomson et al., 2011). The almost doubled decay of the dispersal kernel of *C. chondrilloides* reveals a stronger decrease in seed density with increasing distance from the source (P5). The dispersal distance of both species lies above the average of 2 m (0.1–100 m) investigated for several wind dispersers (Thomson et al., 2011; Stöcklin and Bäumler, 1996). Calculations on the EDD (distance between young plants to the nearest parent) show an overestimation for *M. germanica* (57 m) and a slight underestimation for *C. chondrilloides* (9 m) in comparison to the dispersal distances revealed from seed trapping experiments. The overestimation in *M. germanica* can be attributed to higher wind speed in greater height above ground (Soons et al., 2004) and the longer observation period (seed traps are usually exposed only for a few weeks), increasing the variation in dispersal distances. The EDD does not allow any conclusion on the actual distance travelled by a seed (Jacquemyn et al., 2006), but gives a more realistic idea on the spread of a population. So, for *C. chondrilloides* a progression of the population edge of 5–8 m per year was found (P3), confirming the relatively short dispersal distances of the species and thus a slow spreading rate.

Long-distance dispersal

The role of LDD in the spread of populations remains unclear for the study species. While running water and wind have the potential to carry the seeds over several kilometres, there are many restrictions to these dispersal ways. In natural braided rivers strong winds can transport seeds over larger distances within the open active river corridor, while in degraded rivers higher proportion of proceeded succession stages with shrubs and trees acting as barriers. Colonization of new sites in the course of a flood event can be very successful, as shown for *M. germanica* (P4), but requires the proper timing, flood intensity and river continuum without barriers and flow regulations, making hydrochory less effective in impacted river systems (cf. Merritt and Wohl, 2002).

Seed rain

Beside 'dispersal limitation' restricting the ability of seeds to colonize new patches, 'source limitation' has to be considered, that means, even if the seeds could reach all patches through SDD or LDD, their density is too low to saturate recruitment sites (Clark et al., 2007). An individual of the *M. germanica* can produce about 10,000–200,000 seeds (Bill et al., 1999) resulting in 500–10,000 seeds reaching the edge of the SDD, in contrast to *C. chondrilloides* with on average 100–150 seeds at the edge of the SDD (P3). Seed production is particularly in early successional habitats the limiting factor in the population dynamics of plants (Jacquemyn et al., 2006; Turnbull et al., 2000), and this restriction is even more pronounced in *C. chondrilloides* and additionally amplified by the shorter dispersal distance. It can be assumed for the species, that low seed density at the SDD leads to a slow spread of local populations. The propagule pressure is of high relevance in evaluating the actual population and colonization dynamics. However, since it depends on the population size and fecundity of a local population it is not considered in the assessment of the colonization probability and patch connectivity (P5, P6), that are independent of the actual occupancy of river reaches.

Seedling establishment

As soon as the seeds are exposed to favourable conditions, seeds of *M. germanica* germinate almost within one day, while seeds of *C. chondrilloides* need about ten days. Both study species show high germination rates (>90%) (P3, Sitzia et al., 2021). Germination rate and time is similar to other early alpine colonizers (Marchand and Roach, 1980; Stöcklin and Bäumler, 1996). They can germinate under a wide temperature range and seeds stay viable for months under dry and cold conditions, while seed banks are unlikely (Müller and Scharm, 2001). So under favourable conditions the 'window of opportunity' for the study species to germinate on a suitable habitat comprises a few days on from seed release, underlining the importance of effective dispersal mechanisms and the sufficient availability of recruitment habitat (cf. Balke et al., 2014; Richards et al., 2002). As expected for pioneers on gravel bars, seedling growth is fast, and investment in root growth is relatively high in both species (about 0.10 cm per day during the first weeks) which must help coping with water stress (P3, Sitzia et al., 2021). Consequently, while recruitment itself, in terms of seed viability, germination and seedling growth is not negatively impacted even in small or isolated populations of both species, dispersal distances, seed densities and availability of safe sites, providing sufficient moisture, are most probable limiting factors in colonization.

Colonization potential varies between study species

A successful colonization depends on seedling establishment, which in turn depends on germination, and thus on seed dispersal pattern (Balke et al., 2014). With lower seed production per plant, smaller dispersal distances and narrower habitat niche and mostly inhabiting gravel terraces, where germination and seedling growth depends on safe (moist) sites, *C. chondrilloides* has a lower colonization potential than *M. germanica*. In combination with more specific habitat preferences, the lower dispersal abilities lead to a higher sensitivity to altered habitat configurations (cf. Villard and Metzger, 2014). That leads to a higher vulnerability of *C. chondrilloides* to river degradation and has strong effects on the required connectivity of riverscapes.

Habitat configuration and connectivity of riverscapes

Effects of river degradation and restoration

River degradation was associated with a narrowing of the active river corridor, an increase in vegetated area, so a decrease of the *Gravel Index* (P1), and resulted in lower proportions of suitable habitat for both species (A2, Fig. A2.1, P6). Reduced habitat area was linked to smaller patches, shorter edges and larger distances between patches, that exceeded the species SDD (P6). This unfavourable and more fragmented configuration was expressed in lower connectivity values, varying between the species (A2, Fig. A2.3). Translating the patch distances and dispersal kernels in the *Effective Distance* between patches, differences a higher colonization probability for *M. germanica* (ED < SDD) than *C. chondrilloides* (ED > SDD) showed up. Though, *Effective Connectivity* was reduced along the degraded reach by 70–80% for both species in comparison to the respective reference reaches (P6). Habitat availability is further reduced through a higher number of large gaps (>100 m), that can only be crossed via LDD. For example, the 4 km long degraded river reach is divided by 8 to 17 gaps for *M. germanica* and *C. chondrilloides* respectively (P6). Hence, reachable patches are somehow clustered and the hampered seed exchange among and within patch clusters due to gaps and low patch connectivity further increases the risk of local extinctions (Jäkäläniemi et al., 2005; Volk et al., 2018). Thus, the remaining populations along degraded reaches with unfavourable habitat configuration are most likely in an extinction debt, that often follows habitat destruction (Tilman et al., 1994). For example, in the *M. germanica* population along the degraded river reach proportion of young plants is <10% (Woellner et al., 2019) indicating an overaged population structure, suggesting an ongoing population decline depending on succession speed and longevity of the species.

The river restoration was able to widen the active river corridor, supporting the formation of gravel bars and increasing the *Gravel Index* (P1). In comparison to the degraded reach, the restored stretch provides higher proportion of suitable habitat with larger patches and patch edges and shorter distances (for *C. chondrilloides,* A2, Fig. A2.4). Though, habitat configuration for both species shifted only slightly towards the reference state (P6). It shows better connectivity for *M. germanica* compared to the degraded reach and almost very low improvement for *C. chondrilloides*. Still, the patch network is dissected by fewer gaps (3–8). The referred restoration project with more than 5 km length exceeded the average extent of river restorations (Morandi et al., 2017) and achieved significant improvements in providing pioneer habitats compared to smaller actions and degraded river reaches (P1). The conducted embankment removal was rather successful in restoring gravel bars and suitable habitat for the study species than in the creation of a favourable patch configuration with an appropriate connectivity and colonization probability (P6). The limited success could be due to several factors at larger scale still negatively impacting habitat formation, such as bedload retention and discharge control (Bernhardt and Palmer, 2011; Grabowski et al., 2014).

The given habitat configurations provide lower connectivity for *C. chondrilloides* and thus an overall lower probability of colonization than for *M. germanica*. Thus, the amount of available and reachable habitat is significantly reduced, also through a higher number of large gaps, that can hardly be crossed by the species without extreme events allowing for LDD. Two compounding effects worsen the situation for *C. chondrilloides*: i) more restrictive habitat preferences, that lower the proportion of suitable habitats, which is stronger fragmented, and ii) poorer dispersal abilities lower the colonization potential. To disentangle their relative importance investigations on further river reaches with the species occurrences and integration of temporal data would be necessary.

<u>Further aspects of patch connectivity</u>

So far, the temporal component has been neglected in the investigations of configuration and connectivity. Structural, functional and dynamic connectivity (Zeller et al., 2020) vary along rivers over time. The degree of spatio-temporal connectivity depends on the river dynamics, that effects abiotic and biotic components of connectivity: i) arising of stepping-stone patches, which increases connectivity (Fink and Scheidegger, 2018; Saura et al., 2014), ii) habitat turnover in the sense of shifting gravel bars by erosion and sedimentation without completely destroying them (improving patch habitat suitability), iii) allowing for LDD, that increases connectivity and colonization probability, and iv) varying population sizes and consequently propagule pressure and colonization potential of a local population (Castorani et al., 2017; Zeller et al., 2020). The static consideration of connectivity can lead to an underestimation of patch connectivity by about 30% (Martensen et al., 2017), while divergences can be higher in more dynamic rivers. So, for regulated river reaches (like ‘Lenggries’ in my study) a ‘rescue’ effect by temporal connectivity, so arising stepping-stones and LDD, is unlikely, which underlines the importance of habitat configuration (structural connectivity) for target species populations (Saura et al., 2014).

Further, the calculation on the connectivity was performed, assuming free-dispersal among patches. But, particularly for small-sized wind-dispersers, surrounding vegetation act as barrier for dispersal (Vittoz and Engler, 2007). This matrix-resistance is probably negligible in natural braided rivers with a wide active river corridor with almost only bare gravel areas, but assumable more pronounced in degraded river reaches, where proportion of vegetated area is high and channels are rather oscillating than anabranched (P1). This also lead to a higher importance of hydrochory for LDD compared to far-reaching dispersal through strong winds. Though, wind-dispersal seems to play an important role for LDD in *M. germanica* within and between catchments reflected by its population genetics (Fink et al., 2022; Werth et al., 2014), still its meaning for the colonization of new habitats remains unclear.

Reduced connectivity within populations can impact fecundity and reproduction through inbreeding depression or genetic drift (Jacquemyn et al., 2010). Particularly, if patches are colonized from a few founder individuals and connectivity is not given, low genetic diversity can hamper population establishment (Vandepitte et al., 2012). The thesis related studies show no evidence for the study species to suffer from bottle neck events (P3, P4). Both were found to be able to develop large viable populations from a few founder individuals. In *M. germanica*, genetic diversity of a recently established population at a greater distance from further populations was even higher compared to other large populations within the catchment (P4). Here, connectivity of the reach with only small proportions of suitable habitat would have been considered as low, but unhindered discharge created dynamic (temporal) connectivity to source populations (P4).

<u>Dimensions of fragmentation in river systems</u>

Most likely, habitat loss and the reduction of river dynamics led to past population decline, but current high degrees of fragmentation impede their potential recovery. Fahrig (1997, 2002, 2019) argued in several studies that effects of habitat fragmentation are dismissible against the influence of habitat loss, and several small patches might have the same functionality as a few large ones. This might be true for many ecosystems, but not easily transferable to specialist plant species in dynamic (riverine) systems. Here, due to a non-targeted dispersal of mainly wind-dispersers, colonization probability is strongly reduced between smaller patches just by a lower likeliness of seeds landing on suitable habitat. Further, as shown for the two species in this thesis, bridged distances are in general short and higher patch isolation easily disrupt dispersal chains (P3, P5, P6). Additionally, connectivity reduction is not only caused by a change in habitat configuration, but also by an accompanied alteration of dynamics processes that can temporarily link patches and populations. Fragmentation in terrestrial riverine systems must be considered with respect to patch isolation and disruption of the temporal (lateral and longitudinal) connectivity (cf. Hevroy et al., 2018). The studies constituting this thesis also underline that the strength of the consequences of habitat transformation is strongly species-specific.

Metahabitat configuration in restoration and conservation

Restoring areas, that are actually occupied by human activities is always a trade-off between land use, nature conservation and restoration potential. In rivers this can be applied, for example, to all efforts on re-widening floodplains, that act mainly at the expense of agriculture and forestry. Although widening of the active river corridor is the most effective measure in re-establishing pioneer habitats (Muhar et al., 2016, P1), the extent is strongly limited and reduced to a few cases dealing with only a few kilometres (Habersack and Piégay, 2007; Hohensinner et al., 2018; Morandi et al., 2014, P1). Although, the loss of habitats and species are considered 'the most striking effects' (Habersack and Piégay, 2007) of river engineering, restoration is often unspecific with respect to the species habitat niche and dispersal (Pander and Geist, 2013). For example, restoration of gravel bars must ensure that plant propagules can reach them and that plant establishment is likely. Incorporating a species-centred approach in river restoration is recommended though challenging, because of slightly different habitat niches of the target species. Moreover, there are the unpredictable and dynamic processes acting at the catchment scale (Betts et al., 2014; Kail and Wolter, 2011; Pander and Geist, 2013). The spatio-temporal turnover in habitat availability causes population processes to be controlled on a coarser spatial level, or in other terms, spatial demands of many species refer to habitat availability at the landscape scale (Metzger and Brancalion, 2016; Nagel et al., 2021).

In this thesis the applicability of a species-oriented approach on the landscape level was tested. The respective implications for improved riparian restoration and conservation are pointed out. Thus, a new procedure from identifying species requirements and colonization relevant characteristics to an evaluation of the given habitat configuration and connectivity was developed. The following three steps are suggested:

1. **Determine species-specific habitat requirements**

   Achieve precise estimates of the key environmental parameters, that can be assessed in a standardized procedure, and then used for HSM. Climatic or geologic factors often used in HSM fail to address the spatial scale of metapopulations. Aerial imagery analysis can help to identify relevant structural habitat parameter (P1, P2). For early-successional species on small-scaled patches, data acquirement using drone flights (P2) proofed to be suitable and relevant habitat parameters could be derived. It is important to account for differences between juvenile and adult niches within a species, since it clearly influences colonization relevant habitat availability (P6).

2. **Assess species-specific colonization potential**

Colonization potential of a species can be limited in several critical steps of establishment: fecundity, dispersal, germination, seedling survival, stage transitions to maternity. For early-colonizers with usually high germination rates and seedling survival strongly depending on site conditions dispersal is most limiting in colonization (P3). Dispersal kernels better account for decreasing seed densities from the parent plant than single distance values in modelling colonization probability (P5, P6). Including temporal variations in colonization is highly recommended but only possible under consideration of the given environment and dynamics, that affect LDD events (P4), population sizes or fecundity.

3. **Calculate species-specific habitat configuration and connectivity**
   The rate of seeds that can be exchanged between patches is mostly determined by patch distance and patch shape (affecting exchange-interface length), most important for connectivity of certain configurations (P5). The *Effective Distance* is useful to detect gaps between patches (P5, P6), and priority areas for conservation or reintroductions, with a focus on large and highly connected patches. Also restored reaches can be evaluated, whether they provide a habitat configuration that potentially supports populations of the target species. It is encouraged to incorporate temporal aspects in connectivity analysis, such as frequency of floods that enable creation of stepping-stone habitats or infrequent LDD (P4). Altered river dynamics and barriers (like dams) reduce connectivity. In such impacted river reaches configuration matters more and has to be especially adapted to species colonization potential.

After evaluation of the site conditions, the degree of alteration of the natural dynamics have to be taken into account to achieve effective restoration and conservation (Box 2, Fig. 3.2). The river continuum and flood dynamics (*river connectivity*) can at least partly compensate for insufficient habitat configuration, and allow for colonization process beyond the SDD of the species, also from multiple sources in the catchment (P4). The evaluation of the river connectivity contains a more descriptive analysis of the presence and effects of barriers between populations or reaches with suitable habitats and the flood frequencies.

Box 2: Conceptual model on population conservation in alpine gravel rivers under different degradation scenarios

Shown are four scenarios of river degradation and restoration, including habitat improvements and transplantations.

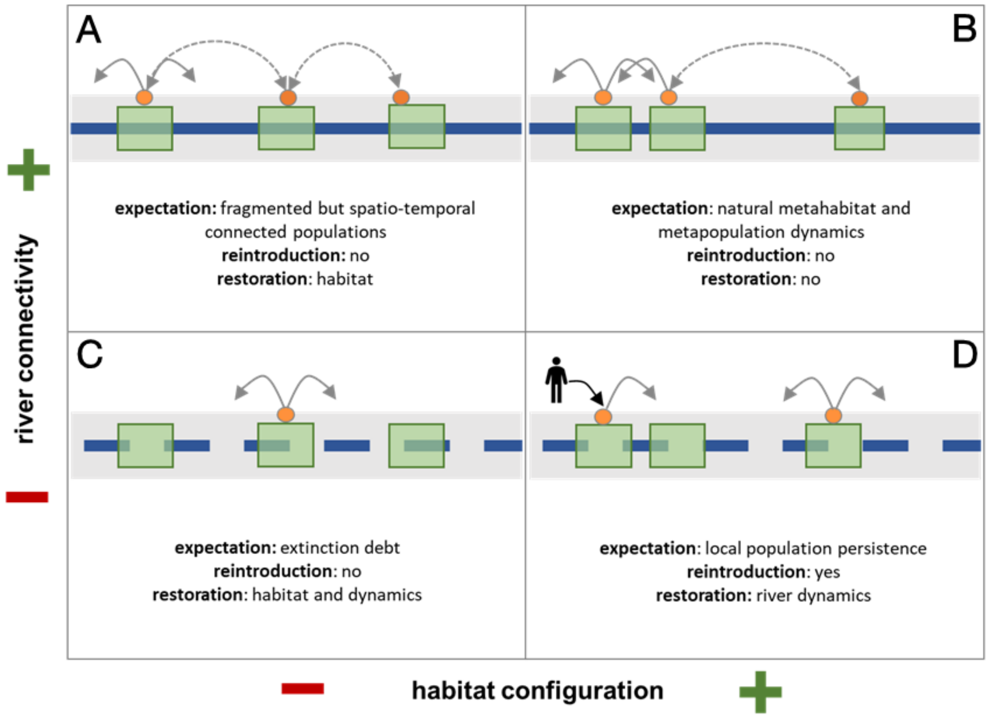


Figure 3.2 Conceptual model on population persistence, reintroduction and restoration derived from the analyses of habitat configuration and river connectivity following a species-centered approach, developed for early-successional plants of gravel rivers (detailed description for A-D in the text below).

(A) Rivers with reduced habitat availability but river connectivity (- +)

Longitudinal shoring (channelization etc.) reduces the active river corridor area and thus the habitat area and further increases the distance between remaining patches (P1, P5). Although, river continuum without barriers can ensure infrequent connectivity to source populations and habitat turnover through flood events (P4). The unimpeded dynamics and passability in the catchment allows for more transient connectivity windows (Zeigler and Fagan 2014), in terms of LDD via floods, that connect isolated habitat patches. Further, with increasing frequency of these events (natural dynamics) a higher connectivity can be reached with the same amount of habitat. So, habitat restoration (by for example river widening) is the base for population establishment, to develop a favorable habitat configuration, but necessary extent of measures decreases with a higher frequency of linking dynamic processes. Reintroductions without restoration is not recommended under insecure connections through (wind or water) flow dynamics, due to low patch connectivity that decrease population persistence probability and thus reintroduction success (Zeigler and Fagan 2014).

(B) Near-natural river reaches with river continuum and suitable habitat configuration (+ +)

Here, human impacts are low, the floodplain provides a large amount of habitat and most of the patches are close to each other with distances below the species SDD. Large populations of the early-colonizers can be expected. The river continuum with natural discharge dynamics connect also isolated patches or distant populations through supporting LDD or the creation of stepping-stone patches (temporal connectivity). Restorations are not required and reintroductions only if a species is not abundant anymore (through former impacts or stochasticity), and source populations are missing in the catchment.

(C) Degraded river reaches with barriers and no or isolated habitats (- -)

Along river reaches, where neither habitats are situated allowing for colonization processes nor the river continuum can support long-distance dispersal or arising of temporal stepping stones, reintroduction cannot be recommended as long as habitat is restored or connectivity via the river dynamics is given. Remaining populations there are most probable into an extinction debt after river degradation took place. Local populations without connection to further patches can survive over longer periods, if the patch is large enough to provide sufficient rejuvenation habitats. But, under hampered river dynamics succession will lower habitat quality for early-successional species over the long-term. Countering succession through scrub-removal for example, as it is reported for preserving local *M. germanica* populations or planting individuals on isolated gravel bars (Woellner et al., 2019), will not lead to self-sustaining populations since it ignores the habitat configuration aspects on a landscape scale. This kind of measure can act as in-situ preservation of a unique genepool, but this should be proofed before planning costly measures.

(D) River reaches with suitable habitat configuration that are isolated from each other (+ -)

Rivers with regional variation in the degree of degradation can have near-natural river reaches supporting populations of endangered species via providing enough available habitat and patch connectivity. Barriers and an altered discharge regime can isolate these reaches from each other and hamper for example recolonization of suitable habitats by disrupting metapopulation structure in the catchment. Here, reintroductions are an appropriate measure, as long as the reaches are large enough to support metapopulation establishment between the connected patches, or if patches are large enough to host large and stable populations. Longevity of these populations depends on turnover of the habitats or migration rate of the gravel bars.

Thresholds for the metahabitat in riverscapes

It can be concluded, that in impacted river systems, spatio-temporal connectivity through river dynamics is reduced and habitat configuration on the reach scale gains in importance for riparian plant populations there. From the presented connectivity indices, the *Effective Distance* could be used for the development of threshold for patch distances, above which a colonization of a certain species is unlikely. This is the case, when population spread mainly depends on SDD and ED >> SDD. To find further critical values the consideration of spatio-temporal aspects is inevitable. For example, there might be minimum sizes of patches or available habitat area enabling population persistence (cf. Collins et al., 2009) by supporting relevant population structures and processes, e.g. genetic diversity or seed production. However, including the occupancy or population data in dynamic systems, a time series is necessary because of their high variations between years, particularly after catastrophic events. Additionally, habitat turnover rates in relation to the species time to maturity and longevity and habitat suitability, determine the requirements on amount of suitable habitat and flood frequencies. For example, in *M. germanica* floods should at least occur every 10–20 years causing a habitat turnover, to counter the decrease in habitat quality due to succession (Gostner et al., 2017). Stelter et al. (1997) also described for *Bryodemella tuberculata* metapopulations on gravel bars a window of optimal flood frequencies (<50-year interval) in relation to the succession speed and the dispersal ability of the species. The assessment of spatio-temporal habitat turnover in relation to floods would also account for the diversity of suitable habitat. Suitable patches can, for example, differ in their height above water table and thus in their turnover rate. When investigating a static habitat configuration without data on temporal changes, suitable patch diversity can help to evaluate local extinction risk. As shown for *M. germanica* (P4), *C. chondrilloides* (P2), and also *B. tuberculata* (Stelter et al., 1997; Wessels and Sundermann, 2022), higher terraces outside a frequent flood dynamic can serve as sources for colonization of nearby arising gravel bars, although they do not provide high quality habitat supporting high rejuvenation rates (P3, P4).

However, the analysis on gaps within the patch network and strength of connectivity between certain patches can help to identify reaches, where reintroductions are appropriate and promising. Endangered species, that are weak dispersers with low fecundity situated in a fragmented riverscape, such as *C. chondrilloides*, require assisted colonization to reach restored river stretches (Renton et al., 2012). Suitability and colonization probability of the river reach can be identified using the connectivity indices (P5), but based on data including habitat turnover for several years. Finding configurations of metahabitats that support very sensitive species in terms of spatio-temporal habitat availability, will optimally benefit further species of conservation relevance.

Concluding remarks

River degradation caused a huge decline of braided river reaches, an extensive loss in gravel bar area and thus pioneer habitats. The cut-off of river reaches through dams and discharge regulations are only one part of the habitat fragmentation that goes hand in hand with habitat loss. In narrower river corridors with high proportions of vegetated area, remaining habitat of endangered early-successional plants is additionally fragmented through gaps between patches that can rarely be bridged by the mostly short-distance dispersal of the species. A further dimension of fragmentation is the decrease in temporal connectivity due to reduced dynamics, that hinders formation of colonisable patches and long-distance dispersal via the water.

It is recommended that a metahabitat concept for species in river systems has to be developed, that goes behind common metapopulation models and allows for an spatio-temporal evaluation of river reaches. Here, not only dams and weirs are considered as barriers, but also gaps between patches within a continuous reach. The various processes causing habitat turnover and their different temporal scales are particularly challenging and they are river-specific. So, simple methods with easy acquirable data are required to answer question for each river (reach) and species of interest, e.g. How long does a patch stay suitable? In which frequency are new reachable patches formed? How is habitat availability changing over time in relation to the species life cycle?

The thesis presents a new combination of approaches to support evidence-based management of river and floodplains, to account for the particularities of plants in dynamic riverine systems. The toolset contains habitat suitability modelling with spatially and temporarily high-resolution data from drone flights and new connectivity metrics, all analysable with standard software in ecology. The procedure is transferable to further plant and animal species in dynamic and patchy systems, and prepared for incorporating the temporal aspects in following studies, which is the next step in the investigations on the metahabitat of riparian plants. The results can support restoration and conservation planning to prioritize actions by identifying spatio-temporal habitat gaps or areas with high probability of long-term population persistence.

Danksagung

Ein großes Dankeschön gilt Prof. Dr. Johannes Kollmann, der mich nach meiner Masterarbeit am Lehrstuhl behalten und ermutigt hat, aus den bisherigen Untersuchungen ein eigenes Forschungsprojekt zu starten. Ich bin ihm sehr dankbar für die Freiheiten und das Vertrauen, diese Arbeit auch unter herausfordernden Bedingungen in der Ferne fertigzustellen.

Ohne ihn wäre die Feldarbeit langwieriger, der Datensatz kleiner und mein Leben um nicht wenige interessante und erhellende Diskussionen ärmer gewesen - ein ganz besonderer Dank daher an meinen Betreuer Dr. Thomas Wagner, für alles!

Vielen herzlichen Dank an meinen Mentor Dr. Andreas Zehm, Prof. Dr. Norbert Müller und Prof. Dr. Michael Reich für ihre ansteckende Alpenfluss-Begeisterung, zahlreiche Denkanstöße und spannende Exkursionen zu Knorpelsalat, Tamariske und co.

Dr. Sabine Fink und Prof. Dr. Christoph Scheidegger danke ich herzlichst für die Möglichkeit eines bereichernden Forschungspraktikums an der WSL, spannende Diskussionen und bleibende Freundschaft.

Danke auch an Dr. Julie Crabot und Dr. Christian Bräuchler für die produktive und unkomplizierte Zusammenarbeit beim Schreiben der Manuskripte.

Weiterhin danke ich allen StudentInnen, die die Promotion mit ihren Projekt- und Abschlussarbeiten unterstützt haben: Lukas Burkel, Sabrina Behrendt, Leonie Schmid, Franziska Ewald, Katharina Beck, Manuel Neukirchen, Jakob Strak, Maximilian Trautner und ganz besonders Christoph Scheuermann für eine einmalige Kajaktour auf dem Tagliamento.

Die Zeit der Promotion haben mir meine MitdoktorandInnen unvergesslich werden lassen. Danke Dr. Katharina Strobl, Dr. Leonardo Teixeira, Dr. Marion Lang, Dr. Alina Twerski, Jakob Huber, Marie-Therese Bleicher, Sandra Rojas Botero und Ferdi natürlich, für den besonderen Wohlfühlfaktor am Lehrstuhl.

Ein großes Dankeschön geht auch an Holger Paetsch, Ingrid Kapps und Kerstin Josten für ihre Hilfe von A, wie Administratives, über G, wie Gewächshausexperimente, bis Z wie Zahlungsangelegenheiten.

Vielen Dank an die Beteiligten des WWF-Hotspot-Projekts, das mir sehr viel Freude bereitet hat und der Ausgangspunkt für das Dissertationsthema war.

Danke an meine Familie, für die verlässliche und liebevolle Unterstützung in allen Lebenslagen, vor allem aber bei der Kinderbetreuung.

Vielen Dank an die Deutsche Bundestiftung Umwelt, die mittels des Promotionsstipendiums die Durchführung meines eigenständigen Forschungsprojekts finanziell erst ermöglicht hat.

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APPENDICES

A1 Characteristics of the study sites

Profiles of the study sites, which were objective of detailed investigations on habitat requirements, habitat configuration and colonization. For each site, coordinates (coordinate system WGS 84), elevation above sea level, reach length, mean annular discharge, mean annual temperature (MAT), mean annular precipitation (MAP) and descriptions of general structures, human impacts and occurrences of study species are given. Aerial photographs origin from Google Earth 2022. Further study sites in the southern Alps that were included in data assessment are shown in Fig. 2.1, and detailed descriptions are available in the appendix of P3.

Flaz		
Coordinates (WGS84)		
Lat: 46°31’36”N	Lon: 9°53’06”E	
Elevation [m a. s. l.]	**Length [km]**	
1710	3.4	
Discharge [m³ s⁻¹]	**MAT [°C]**	**MAP [mm]**
7.7	2.3	710
Description		
In 2003-2004 completely new constructed river course including wider stretches with gravel bar formation.		
Impacts		
Hydraulic blocks stabilize the shoreline along large stretches. No flow or sediment regulation upstream.		
Study species		
Since a large flood in 2004, a *M. germanica* population with > 600 individuals established along the artifical shoreline and on the dynamic gravel bars.		
Related publications		
P4		

References

Vonwiller et al. (2010) Flussbauliches Monitoring am Flaz- Hydraulische 2D-Modellierung und ökologische Bewertung. Wasser Energie Luft, 102, 108-112.
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Friedergries		
Coordinates (WGS84)		
Lat: 47°29'34"N	Lon: 10°57'06"E	
Elevation [m a. s. l.]	**Length [km]**	
940	0.6	
Discharge* [$m^3 s^{-1}$]	**MAT* [°C]**	**MAP* [mm]**
3–5	6.5	1310
Description		
Alluvial fan in the Bavarian Alps in the nature reserve ‚Ammergebirge' with high sediment dynamics and plant biodiversity.		
Impacts		
Embankment of the western shoreline hinders side erosion and might support an incision of the channel. No flow or sediment regulations.		
Study species		
Supports the last remaining population of *Chondrilla chondrilloides* in Germany with > 1000 individuals.		
Related publications		
P2, P3		

References

Wagner, T. C., Zehm, A. (2022) Das Friedergries- Sukzessionskomplex eines alpinen Dolomit-Schwemmfächers. *Tuexenia Beiheft* 14. 25-46.

Isar - Lenggries		
Coordinates (WGS84)		
Lat: 47°36'58	Lon: 11°35'4	
Elevation [m a. s. l.]	**Length [km]**	
710	4.5	
Discharge [$m^3 s^{-1}$]	**MAT [°C]**	**MAP [mm]**
20.7	7.6	1423
Description		
Oscillating river course with single islands, the confined corridor is dominated by willow scrub and forest, few gravel bars with sparse vegetation.		
Impacts		
Sediment retention and discharge regulation by the Sylvenstein reservoir directly upstream the site led to channel incision. Partly embanked shoreline and few sills.		
Study species		
Small population of *M. germanica* (< 100 individuals) with low proportion of young plants		
Related publications		
P1, P5		

References

Maier et al. (2021) Die Obere Isar- eine verlorene Wildflusslandschaft? Eingriffe und deren Auswirkungen sowie Renaturierungspotenziale vom Krüner Wehr bis Bad Tölz. Jb. Ver. Schutz Bergwelt, 86, 3-38.
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Isar - Mühltal

Coordinates (WGS84)		
Lat: 47°59’31	Lon: 11°28’36	
Elevation [m a. s. l.]	**Length [km]**	
550	4.5	
Discharge [$m^3 s^{-1}$]	**MAT [°C]**	**MAP [mm]**
15	7	1426

Description

Oscillating but not anabranching river course with large gravel bars with pioneer vegetation, in large parts already in transition to softwood scrub

Impacts

Restored river reach: embankment removal over >5 km, but sediment retention lead to incision. Residual water stretch with altered discharge dynamics.

Study species

After restoration, a medium-sized population of *M. germanica* (~200 plants) could establish (unclear if spontaneously or assisted).

Related publications

P1, P5

References

Binder et al. (2015) Möglichkeiten und Grenzen der Renaturierung ausgebauter Alpenflüsse- am Beispiel der Isar im Mühltal südlich von München. Jb. Ver. Schutz Bergwelt, 80, 39-62.

Isar - Wallgau

Coordinates (WGS84)		
Lat: 47°32’38”N	Lon: 11°22’20”E	
Elevation [m a. s. l.]	**Length [km]**	
784	13	
Discharge [$m^3 s^{-1}$]	**MAT [°C]**	**MAP [mm]**
4.57	7*	1426

Description

Last remaining braided river reach in Germany, with river dynamics forming open gravel areas and mosaic of successional stages.

Impacts

Residual water stretch, altered flow and sediment dynamics. No lateral embankment and weirs on the whole length.

Study species

It supports the largest population of *Myricaria germanica* in Germany (> 10,000 individuals). A small population of *Chondrilla chondrilloides* was reintroduced in 2018 (< 50 indivduals).

Related publications

P1, P3, P5

* Station Mittenwald-Buckelwiesen (DWD, 1991-2020)

References

Maier et al. (2021) Die Obere Isar- eine verlorene Wildflusslandschaft? Eingriffe und deren Auswirkungen sowie Renaturierungspotenziale vom Krüner Wehr bis Bad Tölz. Jb. Ver. Schutz Bergwelt, 86, 3-38.

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Isar - Vorderriss

Coordinates (WGS84)		
Lat: 47°33’41”N	Lon: 11°27’48”E	
Elevation [m a. s. l.]	**Length [km]**	
741	3.3	
Discharge [m³ s⁻¹]	**MAT [°C]**	**MAP [mm]**
4.57 + flood peaks from Rissbach	7	1426

Description

Last remaining braided river reach in Germany, with river dynamics forming open gravel areas and mosaic of successional stages.

Impacts

Residual water stretch, altered flow and sediment dynamics, but benefits from the tributary Rissbach with high sediment load during floods. No lateral embankment and weirs on the whole length.

Study species

It supports a large population of *Myricaria germanica* (> 1,000 individuals).

Related publications

P1, P3, P5

References

Maier et al. (2021) Die Obere Isar- eine verlorene Wildflusslandschaft? Eingriffe und deren Auswirkungen sowie Renaturierungspotenziale vom Krüner Wehr bis Bad Tölz. Jb. Ver. Schutz Bergwelt, 86, 3-38.

Lech (Tirol)

Lech (Tirol)		
Coordinates (WGS84)		
Lat: 47°25’54”N	Lon: 10°36’38”E	
Elevation [m a. s. l.]	**Length [km]**	
893	5.2	
Discharge [$m^3 s^{-1}$]	**MAT [°C]**	**MAP [mm]**
45	7	1457

Description

Braided river reach with characteristic habitats and species. Restoration was conducted in frame of a EU-LIFE-project in 2001-2006.

Impacts

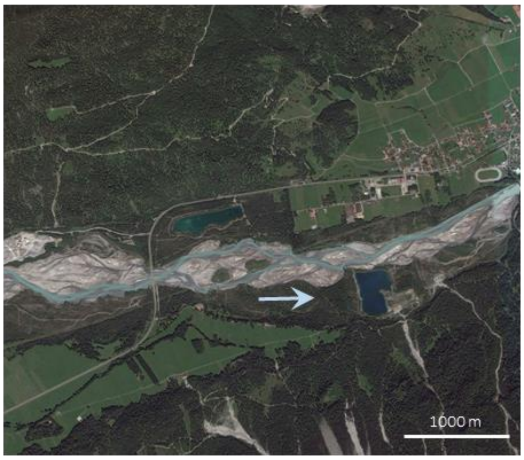
River regulation in the 20th century led to incision and decoupling of floodplain and river dynamics, shift from pioneer to successional stages.

Study species

Large population of *Chondrilla chondrilloides* (>1,500 individuals) used for model validation, large population of *Myricaria germanica*

Related publications

P3, P5



References

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A2 Figures on the comparison of the study species

The figures present data from P1, P3 and P6, consolidated for facilitating the comparison between the study species. They differ in their range of habitat preferences (Fig. A2.1) and their reaction of proportion of suitable habitats and connectivity related to the *Gravel Index* (Fig. A2.2) and their configuration and connectivity related to the proportion of suitable habitat (Fig. A2.3). Further, the configuration and connectivity parameters of the restored reach compared to the natural reference values and the degraded state for each species are demonstrated (Fig. A2.4). For valid statistical analysis more river reaches must be sampled.

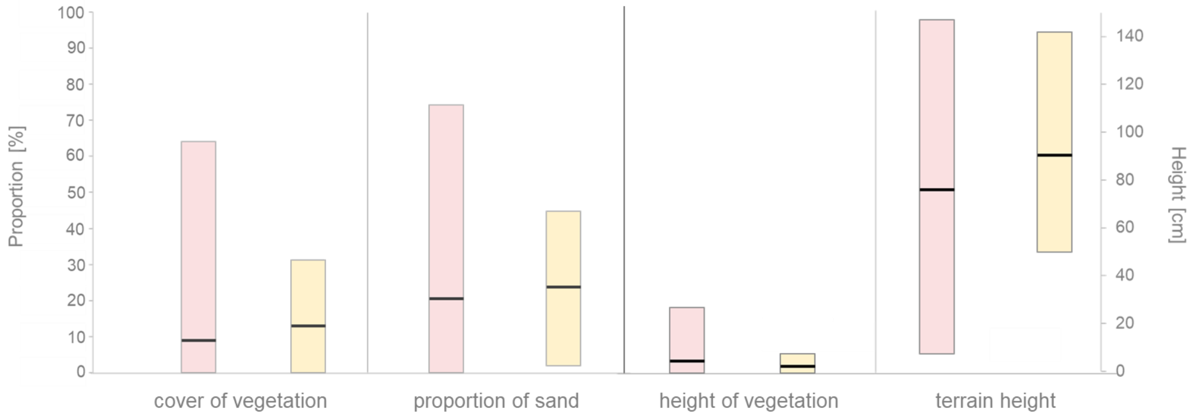
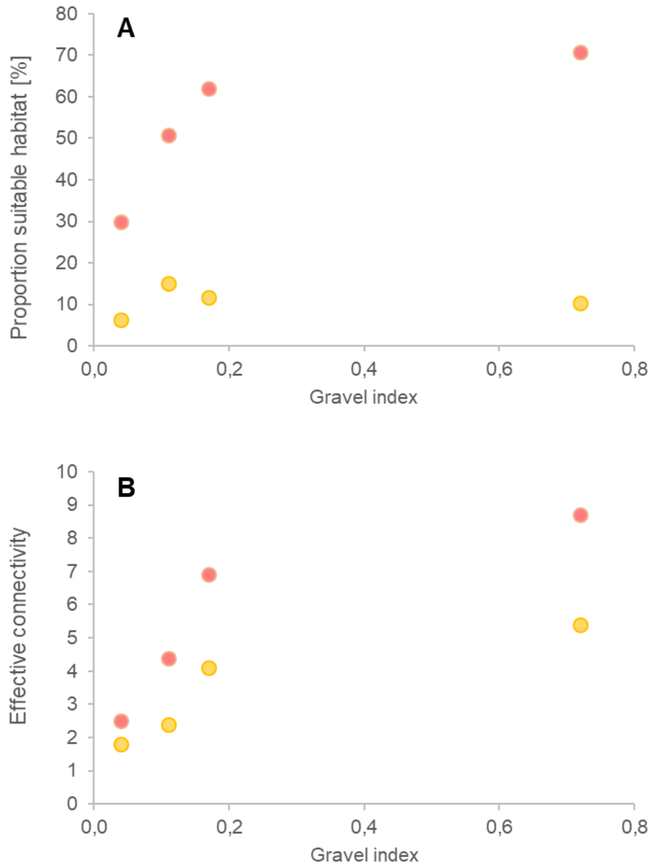
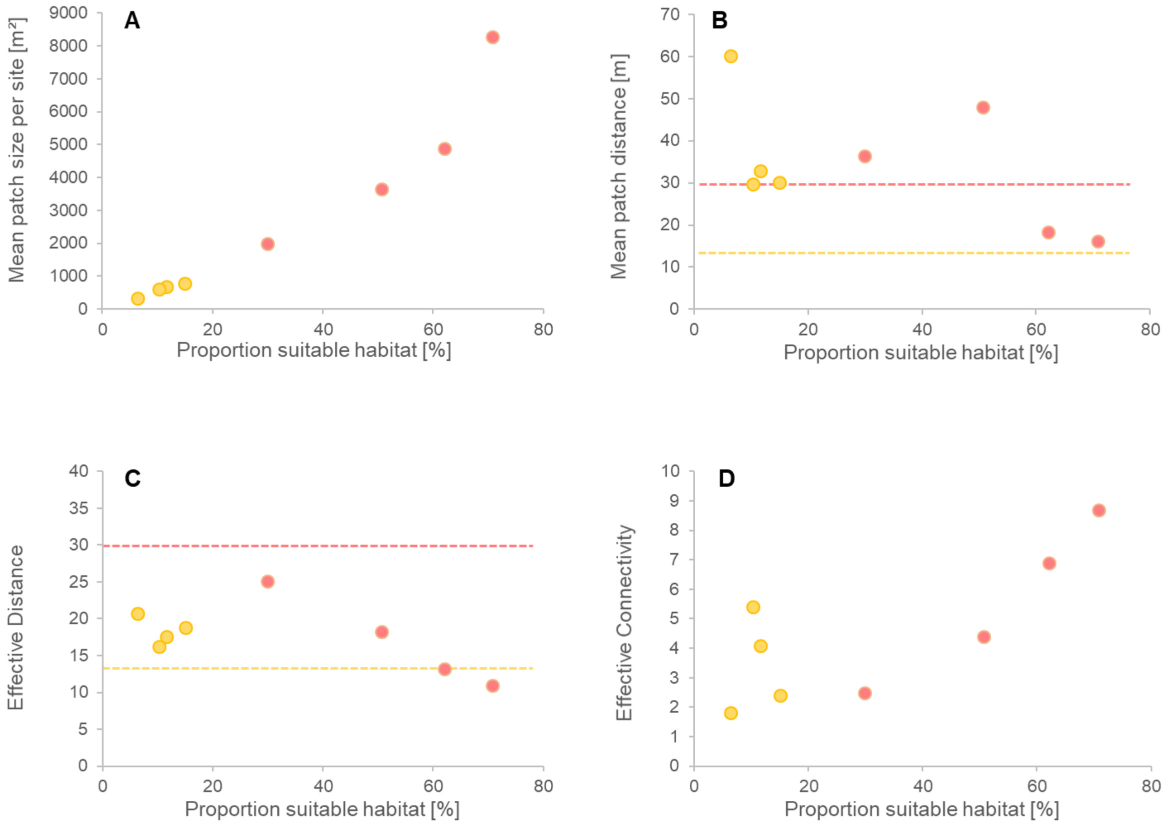


Figure A2.1 Comparison of the habitat niche of *Myricaria germanica* (pink) and *Chondrilla chondrilloides* (yellow) considering the four parameters detected with UAV flights (means and 90% range envelope, both calculated from the habitat suitability model). The range under which *C. chondrilloides* occurs is smaller for all parameters leading through an overall narrower habitat niche of the species.



Figures A2.2 Correlations between *Gravel Index* (P1), proportion of suitable habitat and configuration and connectivity indices (P6) for *Chondrilla chondrilloides* (yellow) and *Myricaria germanica* (pink).



Figures A2.3 Correlations between proportion of suitable habitat and configuration parameters (A, B) and connectivity indices (C, D) (P5, P6) for *Chondrilla chondrilloides* (yellow) and *Myricaria germanica* (pink). Dashed lines show the SDD of the species in the respective colours (P3, P6).

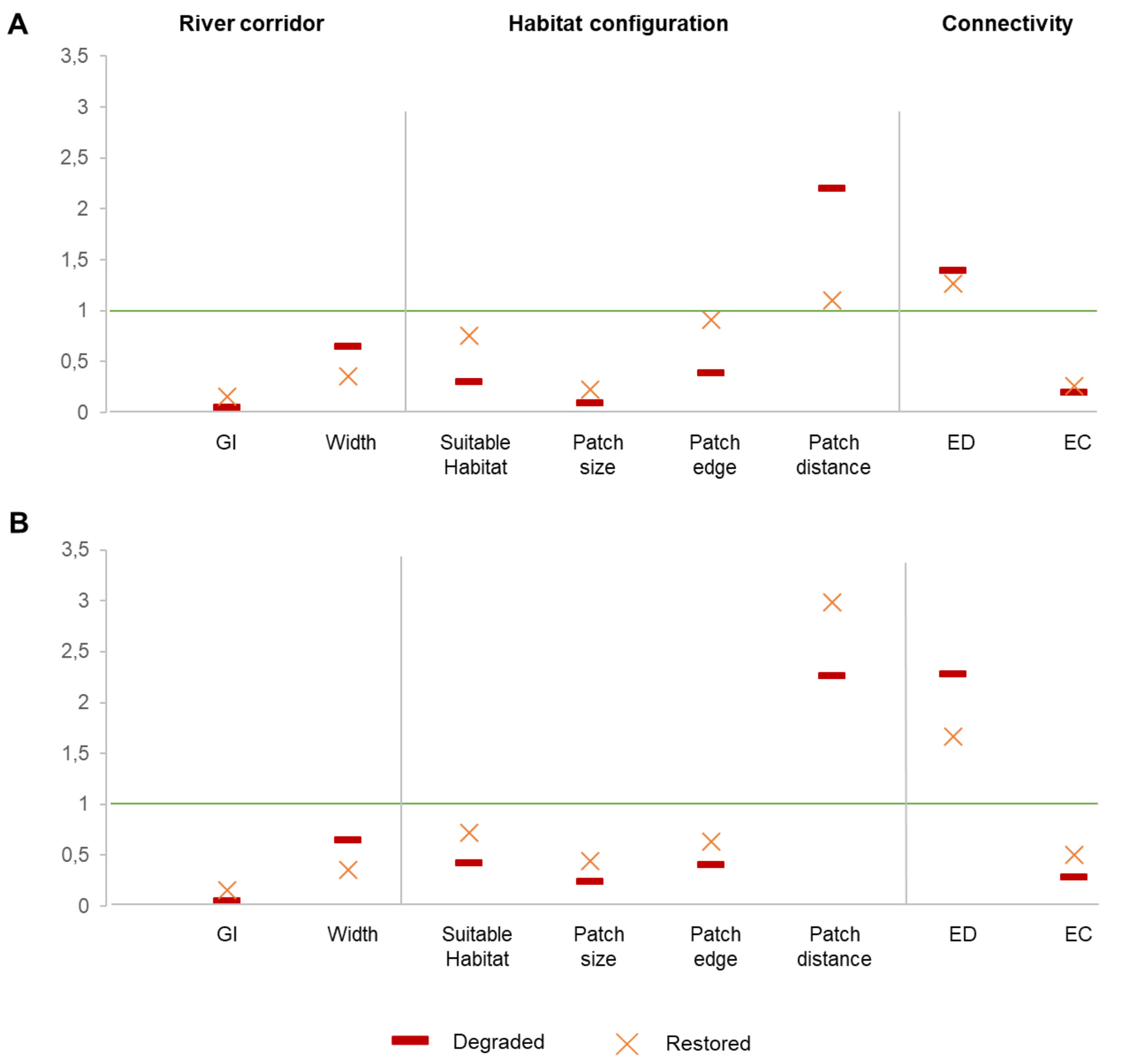


Figure A2.4 Differences between indices of degraded and restored reaches describing river morphology, habitat configuration and connectivity for *Chondrilla chondrilloides* (A) and *Myricaria germanica* (B) in relation to the respective natural reference sites (green line). Indices are *Gravel Index* (GI), width of the active river corridor (P1), proportion of suitable habitat related to active river corridor area, mean patch size, mean patch edge length, mean patch distances, *Effective Distance* (ED), and *Effective Connectivity* (EC, P5, P6).

A3 List of Publications

Peer-reviewed publications

Woellner, R., Wagner, T. C., Crabot, J., Kollmann, J. (2022) Spatio-temporal patterns in degradation and restoration of gravel bars along Alpine rivers. *River Research and Application*, 1–19.

Woellner, R., Bräuchler, C., Kollmann, J., Wagner, T. C. (2022) Biological Flora of Central Europe: *Chondrilla chondrilloides* (Ard.) H. Karst. *Perspectives in Plant Ecology, Evolution and Systematics*, 54, 1–20.

Woellner, R., Scheidegger, C., Fink, S. (2021) Gene flow in a highly dynamic habitat and a single founder event: Proof from a plant population on a relocated river site. *Global Ecology and Conservation*, 28, 1–12.

Woellner, R., Wagner, T. C. (2019) Saving species, time and money: Application of unmanned aerial vehicles (UAVs) for monitoring of an endangered alpine river specialist in a small nature reserve. *Biological Conservation*, 233, 162–175.

Bauer, M., **Harzer, R.,** Strobl, K., Kollmann, J. (2018) Resilience of riparian vegetation after restoration measures on River Inn. *River Research and Applications,* 34, 451–460.
Herrmann, M., Opitz, S., **Harzer, R.,** Totsche, K. U., Küsel, K. (2017) Attached and suspended denitrifier communities in pristine limestone aquifers harbor high fractions of potential autotrophs oxidizing reduced iron and sulfur compounds. *Microbial Ecology*, *74*, 264–277.

Submissions for peer-review journals

Wagner, T. C., **Woellner, R.** (under review) A new set of metrics to quantify the colonization potential of riverscapes by wind-dispersed plant species. Preprint, ResearchSquare. Submitted to *Environmental Monitoring and Assessment*.

Non peer-reviewed publications

Woellner, R., Kollmann, J., Zehm, A., Wagner, T. C. (2020) Gute Aussichten für den Alpen-Knorpellattich in Deutschland? Erste Ergebnisse von Monitoring und Wiederansiedlung lassen hoffen. *ANLiegen Natur,* 42, 1–4.

Woellner, R., Müller, N., Reich, M., Wagner, T. C., Kollmann, J. (2019) Artenhilfsmaßnahmen für gefährdete Wildflussarten – eine Potenzialstudie an den bayerischen Alpenflüssen anhand von vier Beispielarten. *Natur und Landschaft*, 12, 509–516.

Harzer, R., Kollmann, J. (2018) Die letzte Population des Alpen-Knorpellattichs in Deutschland: Gefährdungsanalyse und Förderung der Art. *ANLiegen Natur*, 40, 13–16.

Harzer, R., Müller, N., Reich, M., Wagner, T.C., Kollmann J. (2018) Großräumige Untersuchung von Auenstruktur und Zielartenvorkommen – Empfehlungen für Renaturierungs- und Wiederansiedlungsmaßnahmen. In: Korn, H., Dünnfelder, H., Schliep, R. (Hrsg.) Treffpunkt Biologische Vielfalt XVI Interdisziplinärer Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt. BfN-Skripten 487.

Presentations at international conferences

Woellner, R., Scheidegger, C., Fink, S. (2021) Colonisation and gene flow along an Alpine river. *Annual Meeting of Ecological Society of Germany, Austria and Switzerland,* Virtual, Aug. 30–Sep. 1

Woellner, R., Kollmann, J., Wagner, T. C. (2019) Finding a home in a dynamic environment- Reintroduction of *Chondrilla chondrilloides* supported by UAV surveys. *Annual Meeting of the Ecological Society of Germany, Austria and Switzerland,* Münster, Germany, Sep. 9–13

Harzer, R., Kollmann, J., Wagner, T. C. (2017) Interactions between habitat availability and population dynamics - Floodplain restoration and reintroduction of alpine river plants. *Joint Annual Meeting Ecology Across Borders,* Ghent, Belgium, Dec. 11–14

Harzer, R., Kollmann, J. (2016) Reintroduction of an alpine floodplain specialist - Implications for alpine river restoration? *10th European Conference on Ecological Restoration SER*, Freising, Germany, August 22–26

Poster at international conferences

Woellner, R., Wagner, T. C. (2019) Gewässerstrukturkartierung bedingt geeignet zur Bewertung von Auenlebensräumen. *Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Münster, Germany, Sep. 9–13

Harzer, R., Kollmann, J., Wagner, T. C. (2018) Busting the myth: decline of Alpine river plants and the role of habitat availability. *PopBio*, Innsbruck, Austria, May 3–5