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Dispersal as a limiting factor for colonization of restored sections in mountain streams:

plants & macroinvertebrates

R.J. Brederveld¹, S.C. Jähnig², A.W. Lorenz², S. Brunzel³ and M.B. Soons¹*

¹Landscape Ecology Group, Department of Biology, Utrecht University, Sorbonnelaan 16, 3584 CA Utrecht, the Netherlands
²University of Duisburg-Essen, Department of Applied Zoology/ Hydrobiology, D-45117 Essen, Germany
³Philipps-Universität Marburg, Faculty of Biology, Department of Animal Ecology, Karl von Frisch-Str. 8, 35032, Marburg, Germany

*Correspondence author, email: m.b.soons@uu.nl, fax: ++31 (0)30-251-8366

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Summary

1. In the past centuries European streams have become heavily influenced by humans through pollution and regulation. As a result, the quality and diversity of freshwater riparian habitats has declined strongly, and the diversity of riparian flora and fauna decreased subsequently. Recent restoration measures have resulted in stream habitat improvements, but biodiversity improvements failed to follow in fragmented streams. Dispersal limitation has been suggested to play an important role in the lack of biodiversity improvement in restored streams, but to date there is no conclusive evidence for this assumption.

2. In this study we assess if colonization of restored streams by plants and macroinvertebrates is limited by dispersal. We hypothesize that the colonization success of restored sites increases with increasing ability to disperse over long distances and with decreasing distance of source populations from the site. We compare species compositions in seven restored sections to those of seven nearby unrestored sections and link differences in species’ colonization success to the species presence in the regional species pool, and to the species’ dispersal abilities.

3. Colonization success is highly dependant on abundance in local and regional species pool for both plants and macroinvertebrates.

4. For plants dispersal strategies have an additional influence on colonization success, with short living plants with high production of small, well dispersed seeds colonizing best within the 3-5 year period after restoration which was investigated.

5. The existence of dispersal constraints for macroinvertebrates could not be confirmed. Macroinvertebrates are probably limited by the lack of connectivity on larger spatial scales, but the existence of dispersal constraints for macroinvertebrates could not be confirmed, but beneficial interaction effects of increased plant diversity might improve habitat suitability for macroinvertebrates.
6. Synthesis and applications: Dispersal, by the lack of species’ abundance in regional species pool, is a limiting factor for successful colonization of species in fragmented landscapes. To succeed in restoring fragmented habitats, it is therefore essential to have near-natural areas in the vicinity of restoration projects. Restoration of connectivity on larger scales is essential for improving biodiversity and achieving a good ecological status of restored sites.

Key-words: stream restoration, colonization success, re-colonization, dispersal ability, regional species pool
Introduction

Human impact on landscapes often resulted in degraded landscapes with monotonous landuse and low habitat diversity and, as a result, low biodiversity, biological functioning and ecosystem services (Millennium Ecosystem Assessment M.A., 2005). Especially in freshwater ecosystems, anthropogenic influence strongly affected ecological quality (Giller, 2005; Søndergaard & Jeppesen, 2007). Ecological degradation is problematic as freshwater systems are of great importance, with increasing demand for freshwater and for good quality water, and legislation aiming to achieve this (e.g. EU Water Framework Directive (EC, 2000)). In streams, sewage loading negatively influenced water quality, while modification and regulation resulted in loss of natural flows, and canalization reduced the number and suitability of habitats; all these processes strongly reduced stream biodiversity (Søndergaard & Jeppesen, 2007).

To restore the ecological quality of streams, many river restoration projects have been carried out. Commonly used restoration measures include addition of large wood (Kail & Hering, 2005; Kail et al., 2007), the removal of bank fixation (e.g. Rohde et al., 2005; Formann et al., 2007) and floodplain excavation as well as excision of the riverbed (e.g. Gurnell et al., 2006). The hydromorphological effects of these restoration actions improved habitat number and quality, but failed to positively influence biodiversity in highly fragmented streams (Larson et al., 2001; Rohde et al., 2005; Jähnig, 2007; Spänhoff & Arle, 2007; Jähnig et al., 2008b), although positive biodiversity effects are observed in near-natural streams (Helfield et al., 2007; Kail et al., 2007). It is important for stream restoration to re-introduce habitats, but in heavily fragmented streams this has not always been sufficient to restore and conserve biodiversity (Suding et al., 2004; Hilderbrand et al., 2005; Palmer et al., 2005). Therefore it is necessary to identify the bottleneck for riparian and aquatic organisms. Following restoration projects, habitat availability and quality are generally increased and therefore not likely to
substantially limit recolonization (Rohde et al., 2005; Jähnig, 2007; Kail et al., 2007). Dispersal limitation has been suggested to play an important role in the re-colonization of these restored streams (Rohde et al., 2005): Fragmentation of stream habitats hampers dispersal between patches (Jansson et al., 2000), so species composition is highly dependant on the local species pool (Renöfält et al., 2005; Lake et al., 2007) and dispersal of the organisms (Nilsson et al., 2002).

As dispersal limitation may play a critical role in the lack of success of biodiversity restoration measures in streams, it is important to know how riparian and aquatic organisms disperse. We focus here on two organism groups that are generally used for the assessment of restoration success and as indicators for stream quality: plants and macroinvertebrates (EC, 2000). Dispersal by water (hydrochory) is the most prominent form of plant dispersal in river and stream ecosystems (Leyer, 2006). Passive dispersal of macroinvertebrates occurs on a large scale due to drift in rivers, but also active compensatory upstream movement can be observed (e.g. Elliott, 1971; Turner & Williams, 2000). Dispersal by wind (anemochory) is also relevant by dispersing propagules in lateral directions and to sites not connected to the source population by surface waters (Soons, 2006). In aquatic macroinvertebrates aerial dispersal has been demonstrated as a dispersal vector likely to enhance colonization of patches (Vanschoenwinkel et al., 2008). Dispersal by animals (zoochory) is also often used to explain upstream colonization (e.g. Pollux et al., 2007). Seeds of plants can for instance be dispersed by waterfowl (Figueroa & Green, 2002) and also for macroinvertebrates, bird mediated transport may play a major role (Green & Figuerola, 2005). Although in streams this probably has minor relevance as (mountain) streams are not a major waterfowl habitat. Different dispersal vectors thus have the potential to disperse plant and macroinvertebrate propagules in streams, but fragmentation of habitats in riparian landscapes disrupts each of
these dispersal strategies, reducing colonization ability and species survival (Soons & Ozinga, 2005; Ozinga, 2008).

So far, the theory of dispersal limitation as a critical factor in the recolonization of restored streams has mainly been inferred from lack of colonization after successful habitats restoration. Although the theory appears plausible, direct evidence of dispersal limitation as a critical factor for recolonization is still missing. Therefore, we investigate the role of dispersal as a limiting factor in the colonization of restored streams sections by plants and macroinvertebrates. We hypothesize that the colonization of restored sections increases with a species’ ability for dispersal and decreases with distance to nearest source populations. We study this in seven restored streams, where hydromorphology and habitat heterogeneity have been successfully restored (Jähnig et al., 2008a) and compare the colonization success of plants and macroinvertebrates with different abilities for dispersal and different abundances in the regional species pools.

Materials and methods

Study system

We investigated the restoration success of mountain streams by comparing restored stream sections to unrestored sections. We studied seven paired sites, each with a restored multiple channel (MC) section and nearby unrestored single channel (SC) section, located in the rivers Lahn, Orke, Eder, Nims and Bröl in the lower mountains of the Rhenish Slate Mountains (between 49°56'N - 51°2'N and 6°29'E - 8°51'E). Active restoration measures were taken for three sections in the years 2000-2002, while the other four sections were passively restored by halting floodplain use from 1995 on. All sections were surveyed for hydromorphological features and plant and macroinvertebrate species distributions in 2004-2005, 3-9 years after the start of the
restoration. Results of these surveys show that in comparison to unrestored sections, restored sections had significantly higher numbers of channel elements and aquatic and riparian mesohabitats, but Shannon diversity of aquatic and riparian organisms showed no significant differences (Jähnig et al., 2008b). Biodiversity thus appears to be not restricted by habitat, but might be limited by dispersal, making these sites ideally suited for an investigation on recolonization in stream sections.

To test if colonization of restored stream sections by plants and macroinvertebrates is limited by dispersal, we investigated if colonization success is related to the presence of species in the regional species pool and/or to the dispersal ability of the species. Two methods were used on the data: abundance based regression with high detail and presence/absence based analyses of groups to verify these results.

Colonization success 1 - abundance data

To quantify colonization success at the restored sections we used vegetation and macroinvertebrate survey data of the unrestored and restored sections, collected in 2004 and 2005. The vegetation survey data were collected along ten equidistant 2m-wide transects, perpendicular to the main stream, over a section of approximately 200m length of the main stream (or eight transects in the Lahn-W site due to limited riverbed access). Along each transect vegetation was identified, and length of each vegetation type was measured. For each vegetation type present in a section, a number of vegetation surveys (varying from 1 to 24 surveys, on average 10m²) was taken depending on the total abundance of that specific vegetation type (on average one plot per 7m transect length) (Jähnig, 2007).

To calculate colonization success, abundance of the species in the restored sections was compared to expected species abundance. All surveys were clustered using the classification and twinspan clustering in Juice (Tichy, 2002), in order to obtain the expected plant species
abundances, these clusters were classified using Oberdorfer (1992), using Synbiosys’ species nomenclature (http://synbiosys.alterra.nl/eu/). Species absence/presence data from the vegetation survey plots were used to calculate species abundance per vegetation type. These (expected) abundances were then weighed by total cover of each vegetation type occurrence, to calculate average (expected) abundance of each species for the section. Colonization success was calculated from the vegetation surveys and accompanying expected species abundances as:

\[
\text{Colonization success} = \frac{\text{actual abundance} + 0.1}{\text{expected abundance} + 0.1}
\]

(equation 1) (small constants were added to avoid division by zero).

Colonization success 2: presence/absence data

For the macroinvertebrates, detailed data on expected abundances were available (Haase et al., 2004), but not comparable to the macroinvertebrate survey data (see below). Therefore, we adopted a second approach to quantify colonization success and applied this to both plant and macroinvertebrate data. For this analysis, we grouped all present and expected species in four groups and compared these among each other: 1: species present in both unrestored and restored sections, 2: present in unrestored section, but not in restored section, 3: present in restored section, but not in unrestored section, 4: expected to be present in restored section, but not present. Expected presence of plant species was determined from vegetation types and expected presence/absence in these following Oberdorfer (1992; see above).

The macroinvertebrates survey data were obtained using a shovel sampler (500μm mesh size, 0.0625m² sampling area) according to the multi-habitat sampling protocol (Hering et al., 2003), taking a sample on each of the different substrates present in the plots. The high level of detail from this survey (Jähnig & Lorenz, 2008) makes the data not directly comparable to the stream reference image (leitbilder, Haase et al., 2004), but species presence/absence can well be compared. The expected presence of macroinvertebrate species was determined from
the habitat surveys and species composition from the stream reference (stream type nr 9, Haase et al., 2004). Abundance data were available, but scored to binomial scales for analysis. Before data analysis all species lists were adjusted to the same taxonomic identification level.

Presence in the regional species pool

As a potential explaining factor for colonization success, we quantified availability of sources of possible colonizers at three distances from the restored site: 1) species’ abundance in the unrestored section (local species pool, at max a few 100m distance), 2) species’ presence/absence in the direct surrounding area (medium-scale species pool, within 5x5 km) and 3) the relative abundance of species in a wide surrounding area (large-scale species pool, within 25x25km).

For plants, the first parameter was derived from the species survey in the unrestored section, the latter two parameters were scored using the distribution of plant species following flora atlases of the area at a 5x5 km resolution (Becker et al., 1996; Haeupler et al., 2003). Due to missing species distributions for two sites herein, the regional species pool could not be constructed for the sites Lahn Cölbe and Nims; therefore these sites had to be discarded from further analyses for plant data. Presence in the regional species pool was scored on a binomial scale (presence/absence) for the medium scale distance and as an abundance fraction in the 25x25km area for the large scale distance.

For the aquatic macroinvertebrates also the species abundance at the unrestored section was used as local species pool. The large-scale species pool was derived from a large database with macroinvertebrate survey data (J. Böhmer, unpublished data, 2008), using recordings from surrounding 25x25 km region. Relative abundances in the 25x25 km grid were calculated from all recordings; within the 5x5 km grid insufficient data were available.
Dispersal ability

To determine the dispersal ability of the species involved, databases on several dispersal traits available were used. We selected species traits to quantify the different stadia of dispersal. For the plant species: seed production and life span to estimate propagule source strength; floating capacity, wind dispersal ability and seed longevity to describe spatial and temporal dispersal of these propagules; and habitat requirements, to correspond to germinating and growing conditions of the dispersed propagules. This resulted in the use of the following available variables: Seed mass (mg), Seed number per individual (count), plant life span (converted to ordinal scale: annual (1), strict monocarpic bi-annual (2), perennial (3)), seed terminal velocity (m/s), seed buoyancy (percentage of floating seeds after one week), all from the LEDA plant traitbase (Knevel et al., 2003; Kleyer et al., 2008); seed bank type (ordinal scale: (1) transient, (2) short term persistent, (3) long term persistent, from Thompson et al., 1997), and Ellenberg indicator values for moisture and nutrient requirements (ordinal scale, resp. 1-12 and 1-9, from Ellenberg et al., 2004).

For aquatic macroinvertebrates: life duration, aquatic locomotion ability and aerial dispersal ability were used as dispersal traits in the analysis. Life duration was converted to a binomial score (>1yr: (1); <1yr: (0)); Aquatic locomotion type traits were weighed (swimming/seating: (2); swimming/diving: (2); burrowing/walking: (1); sprawling/walking: (1); (semi)sessile: (0)) and summed to produce a locomotion score, both traits from Freshwaterecology.info (Euro-limpacs Consortium, 2008). Aerial dispersal ability was scored using aerial stage information (no/yes) and flight ability (bad/good) to an ordinal scale ((0) no flight ability, (1) poor flight ability (2) good flight ability; A.W.Lorenz, unpublished data, 2008).

Data analysis
Before analysis correlations between individual parameters were calculated. To detect
effects of presence in the regional species pool and dispersal ability on colonization success,
we used two methods: multiple regression to model colonization success on a continuous
scale (only for plant data) and ANOVA to investigate differences in species traits between
discrete quantified groups with different colonization success (plant and macroinvertebrate
data). Both methods provide complementary information, respectively on the involvement of
variables in the colonizing success and the comparison of those parameters in a quantitative
manner.

The multiple regressions were used to build models with the regional species pool data,
abundance at SC section and species’ dispersal traits as explaining variables in a multiple
stepwise regression. As dependent variable we used the colonization success indicator
(equation 1). Regression residuals were checked for normality, also intercorrelation levels
were acceptable.

The ANOVAs were carried out nonparametrically due to non-normality and
heterogeneity within groups. We tested if there are differences in average dispersal ability and
presence in the regional species pools between the different categories using Kruskal-Wallis
tests in combination with Bonferroni corrected pairwise Mann-Whitney U tests. Differences
between groups for macroinvertebrate data calculated non-parametrically for continuous
variables (regional species pool, locomotion type) and as a Pearsons chi square for ordinal
data (aerial dispersal ability, life duration). Due to a low number of observations in groups 2
& 3 (present only in unrestored section (0) and present only in restored section (11)
respectively), only differences between group 1 & 4 could be calculated.

Data were transformed for statistical analysis when necessary: colonization success,
seed mass, seed number and seed bank type were log10 transformed, buoyancy was square
root arcsine transformed. All statistics were calculated with the SPSS 15.0 package (SPSS, 2006).

Results

In total, 1970 plant and 1178 macroinvertebrate (actual & expected) colonization events (presence/absence of species in a section) were analyzed.

Correlations between species pools and dispersal traits

For the plant species SC abundance, presence in 5x5 km grid and abundance in 25x25 km grid were significantly positively correlated (Table 1A), indicating that species present in the SC section correspond to the species in the regional species pools and vice versa. Plant dispersal traits also showed strong correlations among each other (Table 1B), indicating the existence of different life history strategies: seed mass is negatively correlated to seed number, indicating that species with light seeds produce more seeds, which are also well-dispersed by wind (positively correlated to terminal velocity), float well (negatively correlated to buoyancy) and are persistent in the soil seed bank (negatively correlated with seed bank type). Particularly, species with persistent seeds are also short living species (negative correlation between seed bank type and life span). Also interesting is the high positive correlation between buoyancy and Ellenberg indicator value for moisture, which could be an indication for wet growing conditions and high potential for water dispersal.

For macroinvertebrate species SC abundance and abundance in the 25x25 km grid were significantly positively correlated (Spearman r=0.609, p<0.001, N=1178), showing that the species in the local species pools match to the species in the regional species pool closely. Macroinvertebrate life traits also show high significant positive correlations (Table 2) between life duration and locomotion type and also between locomotion type and aerial
dispersal ability, suggesting that macroinvertebrates that are more mobile in the water also
have a higher aerial dispersal ability.

Colonization success 1- Regressions
For plants, linear multiple regressions executed for each site separately and for all sites
joined (Table 3) show plant life span and SC abundance as included variables in all
regressions. Furthermore seed mass, abundance in the regional species pool (25x25 km grid),
seed bank type, Ellenberg indicator for moisture and nutrient requirements are parameters
significantly related to colonization success. Abundance in the SC section (short-distance
species pool) is positively related to colonization success and life span predominantly
negatively, indicating that colonization mainly occurs by species already present in the nearby
species pool and by species with short living individuals. Seed mass is negatively related to
success of colonization and seed bank type positively, indicating that species with smaller
seeds and long-term persistence in the seed bank are more successful in colonization of
restored sites. The large scale species pool (25x25 km grid) is also positively related to
colonization success, showing that abundance in the regional species pool is another
determinant of colonization success in restored sites.

Colonization success 2- Nonparametric ANOVAs
For the plant species, the four groups reveal differences for most of the species
parameters: there are significant differences between the groups (Fig. 1) in presence in the
regional species pool (5x5 grid, p>0.001) and 25x25 grid (p<0.001), seed mass (p<0.001), life
span (p<0.001), seed bank type (p<0.001), Ellenberg moisture (p<0.001) and Ellenberg
nutrient (p<0.001) values. Seed number was shown as marginally significant (p=0.044), but
failed to show significant contrasts.
Regional species pool data at both medium- and large-scale distances show species found in both unrestored and restored sections also have the highest regional abundances, whereas the expected species have the lowest regional abundances. This means that the species that colonize the least well are the species with the lowest abundances in the regional species pools. Seed mass of the species in the restored sections is lowest, while expected but not-present species have the highest seed mass, implying that colonization occurs predominantly by species with low seed mass. A similar pattern can be seen for life span: species best able to colonize restored sites have the lowest life spans. Seed number and seed bank type show inverse patterns, indicating that the species most able to colonize the restored sections have greater seed numbers and higher seed bank persistency.

Ellenberg indicator values for moisture requirements show a trend to of being lower in the species only in the restored section and in the expected species group. Ellenberg indicator value for nutrient requirements is highest in the group of species found in both sections, and significantly lower in the other groups. The seed dispersal traits terminal velocity and buoyancy show no relation to colonization success.

For macroinvertebrate species, there are significant differences between groups for abundance in the 25x25km regional species pool and for aerial dispersal ability (Fig. 2). Abundance in the regional species pool is higher for species which are found in both sections compared to the species expected but not found. Also the low number of observations in the groups which are only found in SC or in MC section shows that if species occur, they are mostly found in both sections. Similar to the plants this means that the species that colonize best are the species with the highest abundances in the regional species pool. The aerial dispersal ability is higher for species expected to be found in comparison to the species occurring in both SC and MC section, which contrasts expectations in case of dispersal ability limitation. There are no differences in life duration or aquatic locomotion.
Discussion

To investigate if dispersal is the limiting factor in colonization of restored stream sections by plants and macroinvertebrates, we tested the relation between colonization success and dispersal limitation. Dispersal limitation can be hypothesized to occur due to limitation of propagule sources or limitation of the dispersal process, therefore colonization success in relation to the presence of species in the regional species pool (limitation of propagule sources) and the dispersal ability of the species (dispersal ability limitation) was investigated.

Our results show that abundance in the local and regional species pool is an important factor to predict colonization success: species with a higher abundance in the surrounding area are more likely to colonize restored sections. This means that either there is strong dispersal limitation in the form of source limitation, or the species that fail to colonize have such specific habitat requirements that they hardly meet any suitable sites in human-dominated, fragmented landscapes – or both. In the case of the plant species the latter two assumptions are unlikely because the species that do not colonize (group 4) have no different habitat requirements than species that colonize (group 3). However for the macroinvertebrates, specific habitat requirements cannot be ruled out and may contribute to our findings. In any case, to succeed in restoring fragmented streams, it is therefore important to have at least well developed vegetation communities in the vicinity of restored areas and this is probably similar for macroinvertebrate communities (Rohde et al., 2005; Jähnig, 2007).

Also dispersal ability parameters appear to be important factors for colonization success in plants. This appears to be a reflection of strategies: suites of related traits which are successful in colonizing restored stream sections. Plant species with high colonization success are short living species and produce many light seeds (see also Henery & Westoby, 2001). Small, light seeds disperse well with different vectors: with wind due to low terminal velocity (Soons et al., 2004), in water owing to high buoyancy, in waterfowl due to unimpaired gut
passage (Soons et al., 2008) and in time, due to high persistence in seed bank (Thompson et al., 1997). This trade-off closely resembles that of r-selected species, implying the ubiquity of such a strategy by successful colonizing dynamic environments.

Surprisingly, plant species that did not colonize show no difference in terminal velocity and buoyancy compared to the other species. These results arise from a bias in available data for these plant traits: most data are collected on good dispersers, i.e. species with low terminal velocity and high buoyancy. Seed mass for species with terminal velocity data available is significantly lower compared to species missing terminal velocity data ($p<0.001$), also for buoyancy, the species with buoyancy data available are no representative subset compared to the total species list ($p<0.001$). Given that almost all data available on these traits are thus for well-dispersed species, these variables logically reveal no significant differences between the groups. Further data collection on dispersal traits is therefore required for an improved analysis on these traits.

Due to the insignificance of the difference between restored and expected but missing groups, habitat limitation is probably of minor importance for colonization success after restoration, suggesting success of the restoration measures in restoring favorable habitat and supporting the validity of the detection of dispersal limitation.

For macroinvertebrates dispersal parameters were generally without significance, except for aerial dispersal ability. The latter is opposite of what would be expected, and can be either caused by lower abundance of species with high aerial dispersal ability in the surrounding species pool due to lack of connectivity, or by more specific habitat requirements of flying macroinvertebrates. Regional species pool is positively and significantly related to aerial dispersal ability ($\phi$ (nominal correlation) $r=0.564$, $p=0.016$), pointing towards habitat limitation. Macroinvertebrates are evidently capable of (fast) dispersal over more than a few tens of meters (Griffith et al., 1998; Petersen et al., 1999; Cohen & Shurin, 2003; Petersen et
al., 2004), but are probably limited by the lack of connectivity on larger spatial scales, in such way that their dispersal distances are outweighed by the distances between habitat remnants in the fragmented study landscapes. This may imply that even for well-dispersing aquatic macroinvertebrates habitats are currently isolated (see also Soons et al., 2005), although further research is needed on dispersal in aquatic macroinvertebrates (Malmqvist, 2002; Bohonak & Jenkins, 2003). There are indications that macroinvertebrates benefit from microhabitats created by colonizing plants, for large wood and living parts of plants are additional high quality substrates for macroinvertebrates in restored sections (Jähnig & Lorenz, 2008). Therefore increasing plant diversity in restored sections might interact with macroinvertebrate diversity by enhancing habitat diversity and ameliorate biotic constraints towards suitable conditions for macroinvertebrates.

In conclusion, dispersal limitation appears to be a determining factor for colonization success in restored streams by plants: their colonization is limited by (lack of) propagule source in the surrounding area and dispersal ability favoring short living, well dispersing life history strategies. These results are in agreement with a recent study by Kirmer and colleagues (2008) on dry ecosystems.

Dispersal limitation for macroinvertebrates is not unarguably demonstrated, but data available at least suggest the limitation by availability of propagule sources in the relevant species pools. Dispersal ability data available did not show a limitation in the dispersal capacity, but also might be caused by the general lack of information available on dispersal in macroinvertebrates. Other factors like area or habitat requirements necessary for reproduction may play an important role in recolonization. Nevertheless, macroinvertebrates can take advantage of increasing plant colonization for plants can create suitable microhabitats for macroinvertebrates.
Therefore to improve success of restoration projects by improving biodiversity present, dispersal limitation, due to propagule source limitation and dispersal ability limitation, has to be taken into account. Consequently to overcome propagule source limitation, it is crucial to strategically plan restoration areas within the reach of (natural) areas with potential source populations (Soons, 2006; Kirmer et al., 2008). After making this first step, creation of stepping stones (Jähnig & Lorenz, 2008) of restored areas can be a successful way to shorten distances and improve connectivity between dispersal kernel and restoration area. Dispersal as limiting factor for the colonization of restored stream sections is mainly a problem in landscapes with high habitat fragmentation and scaling-up of restoration projects is of major importance for improving biodiversity and achieve good ecological status of streams in near future. To surmount the limitation in dispersal ability, species with low colonization potential, e.g. species with high seed mass and therefore high terminal velocity and low buoyancy or species with long lifespan and short seed bank persistence, have to be aided to colonize restored sites (e.g. Patzelt et al., 2001; Hulme, 2005; Donath et al., 2007). Alternatively autonomous colonization may take a very long time.

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References


Tables

Table 1 A: Spearman correlations between plant species distribution data show significant correlations between abundance in single channel (SC abundance), presence in 5x5km grid and 25x25km species abundance (for all sites combined, N=1970). B: Spearman correlation matrix for plant species traits shows significant correlations between most traits. *: p < 0.05; **: p < 0.01; ***: p < 0.001.

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<td>0.194***</td>
<td>0.148***</td>
<td>0.124**</td>
<td>-0.262***</td>
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<tr>
<td>Ellenberg Moisture</td>
<td>N=1735</td>
<td>-0.169***</td>
<td>-0.006</td>
<td>0.111***</td>
<td>-0.007</td>
<td>-0.085**</td>
<td>0.276***</td>
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<td>Ellenberg Nutrient</td>
<td>N=1715</td>
<td>0.115***</td>
<td>-0.105**</td>
<td>-0.092***</td>
<td>0.104***</td>
<td>0.031</td>
<td>0.002</td>
<td>0.200***</td>
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</tbody>
</table>
Table 2: Phi (nominal) correlation matrix for macroinvertebrate species shows significant
correlations between aquatic locomotion, life duration and aerial dispersal ability. ***: p<0.001.

<table>
<thead>
<tr>
<th></th>
<th>Life duration</th>
<th>Aquatic locomotion</th>
<th>Aerial dispersal ability</th>
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<tr>
<td>Life duration</td>
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<tr>
<td>N=256</td>
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<td>Aquatic locomotion</td>
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<tr>
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<td>0.761***</td>
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<td>Aerial dispersal cap.</td>
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<td>N=1178</td>
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Table 3: Regressions on colonization success for the separate sites and all sites joined show life span and single channel abundance (SC abundance) as significant parameters in every stepwise regression (in bold). Further parameters included in models are Regional abundance in 25x25km grid, Seed mass, Ellenberg Moisture, Seed bank type and Ellenberg Nutrient.

<table>
<thead>
<tr>
<th>site</th>
<th>Regression statistics</th>
<th>Variables included</th>
<th>Standardized regression coefficient</th>
<th>p</th>
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<tbody>
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<td>B</td>
<td>(R^2=0.262) p=0.000 df=176</td>
<td>25x25 grid B</td>
<td>0.230</td>
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<tr>
<td></td>
<td></td>
<td>Life span</td>
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<tr>
<td></td>
<td></td>
<td>SC abundance B</td>
<td>0.008</td>
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<td></td>
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<td>Seed mass</td>
<td>0.087</td>
<td>0.021</td>
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<tr>
<td>O</td>
<td>(R^2=0.249) p=0.000 df=187</td>
<td>Life span</td>
<td>-0.266</td>
<td>0.000</td>
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<tr>
<td></td>
<td></td>
<td>SC abundance O</td>
<td>0.254</td>
<td>0.000</td>
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<tr>
<td></td>
<td></td>
<td>Seed mass</td>
<td>-0.200</td>
<td>0.002</td>
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<tr>
<td></td>
<td></td>
<td>25x25 grid O</td>
<td>0.356</td>
<td>0.002</td>
</tr>
<tr>
<td>E</td>
<td>(R^2=0.223) p=0.000 df=181</td>
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<td>Ellenberg Moisture</td>
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<td>W</td>
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<td></td>
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<td></td>
<td></td>
<td>Ellenberg Nutrient</td>
<td>0.073</td>
<td>0.012</td>
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</tbody>
</table>
Figures

Figure 1: Means ± standard errors for different plant species’ parameters show significant differences between groups for some parameters. Group numbers: species 1) present in both sections, 2) present in unrestored section only, 3) present in restored section only, 4) expected to be present in restored section, but not present. Significant differences are indicated with different letters.
Figure 2: Means ± standard errors for different macroinvertebrate species’ parameters show significant differences between groups for some parameters. Group numbers: species 1) present in both sections 4) expected to be present in restored section, but not present. Significant differences are indicated with different letters. Group numbers 2 & 3 had low number of observations and were therefore omitted.