Reinstating longitudinal ecological connectivity in major river restoration projects: land improvement as a tool to create a biodiversity buffer outside levees

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Abstract

River restoration projects are often accompanied by major land improvements, notably of adjacent farmland, which offers the opportunity to create an extensively-managed buffer zone outside the levees that provides valuable micro-habitats for endangered terrestrial and semi-aquatic biodiversity. Land improvement might thus not only contribute to better integrate the newly restored river into the adjacent landscape, but also to reinstate the longitudinal ecological connectivity that crudely lacks along channelized rivers. Based on a theoretical re-allocation of agricultural land via land improvement, we simulated such a longitudinal biodiversity-friendly grassland buffer along a stretch of the Rhône River (SW Switzerland) where a major revitalisation project is under development. We selected a series of locally rare emblematic species and designed a palette of microhabitats, and combinations thereof, to be created for reaching these biodiversity targets. Estimations of species-specific habitat patch size requirements as well as dispersal abilities were used to analyse what would be an optimal spatial connectivity for such microhabitats. Since such a buffer zone will necessarily stretch along the riverbed, we tested, via a metapopulation model, whether arranging key habitats longitudinally implies different spatial constraints and planning strategies than positioning them in an isotropic context. Simulations showed that these differences were negligible at the foreseen scale. We conclude that land improvement could be instrumental to restoring ecological connectivity in major river revitalisation projects. We also provide concrete quantitative values for restoring an optimal ecological buffer along the Rhône that will promote locally endangered biodiversity.

Keywords: Hanski metapopulation model, grasslands, buffer zone

Introduction

Rivers are key biodiversity hotspots but also among the ecosystems most affected by human activities (Vitousek *et al.* 1997; Revenga *et al.* 2000). More than 70% of the large rivers of Europe, North America and the former Soviet Union are strongly regulated today (Dynesius & Nilsson 1994) while over 90% of the European riverine floodplains have been degraded or destroyed (Tockner & Stanford 2002). This has led to a major decline in riverine, riparian and floodplain biodiversity (Paetzold, Yoshimura & Tockner 2008). To restore ecosystem functions and protect river surroundings, notably human infrastructures, from increased flood recurrence, river restorations have accelerated in the last few decades (Giller 2005). Although there already exist scientific guidelines for successful river revitalization (Palmer *et al.* 2005), most projects today focus principally on enlarging the riverbed. To restore the fluvial processes and reinstall natural riparian communities, however, this is rarely enough. Under current circumstances, in effect, it is hardly achievable to reconstitute the whole range of riparian habitat types (i.e. the different stages of vegetation succession) as land use for human activities represents a major spatial constraint (Gillilan *et al.* 2005).

All the more it is important to develop a guiding image for creating riverine and riparian ecosystems that provide maximal benefits for biodiversity and ensure the persistence of crucial ecosystem services such as river regulation. An important point of habitat recreation, especially in river dynamics, is ecological connectivity. According to Ward (1989), there are four different types of connectivity in lotic systems. First, the longitudinal connectivity describes the occurrence of habitats along the course of the river. Second, the lateral connectivity assesses the connection between the river and the surrounding habitats. Third, the relationship between the groundwater and the surface water is described as vertical connectivity; and, lastly, the temporal connectivity observes the dynamics of the system over time.

These different connectivities, in particular longitudinal and lateral connectivity, would be enhanced if a biodiversity-friendly buffer zone outside the levees would be planned in addition to river widening (Fig.1). Such a buffer zone can help rebuild various riparian habitats along the river offering different successional stages and contribute to better integrate the new river into the wider landscape (Ward & Tockner 2001; Ficetola, Padoa-Schioppa & De Bernardi 2009). The goal of any restoration should be to create a dynamic landscape mosaic with complementary habitats. Although they do not touch the riverbed itself, land improvements often accompany large river restoration projects. Providing that they integrate modern ecological thinking, they may serve as a tool for biodiversity conservation by rebuilding valuable habitat mosaics, notably for terrestrial and semi-aquatic biodiversity. It is clear that some natural dynamics will remain difficult to implement outside the levees. An option would consist in creating an extensively-managed grassland buffer zone, punctuated with key microhabitats, adjacent to the river outside the levees. These key microhabitats are natural structures particularly important for biodiversity (ponds, stone piles, bushes, etc.), which are now absent from modern alluvial plain landscapes.

In this study, a theoretical re-allocation of agricultural habitats, as typically resulting from land improvement operations, was simulated across the plain of the lower Rhône valley (Valais, SW Switzerland) to model a possible grassland buffer zone along the Rhône River. The river was straightened and embanked during two major correction operations in the 19th and 20th century (Summermatter 2004; Canton-of-Valais 2015). After some severe floods and dam failures, particularly at the end of the 20th century, a third major river correction was planned. Its concept and funding were accepted by Valais citizens in a democratic vote in 2015 and first urgent restoration measures to combat flood hazard are currently being implemented. Yet, in the mid and long term, the target is not only to protect human infrastructures and economic activities from future floods, but also to compensate the numerous ecological deficits that emerged after the former two, much too drastic river bed corrections (Canton of Valais 2015). Associating a biodiversity-rich, extensively-managed agricultural buffer zone (equipped with specific microhabitats) outside the embankments all along the river, where feasible, would represent a major biodiversity asset, by dramatically enhancing longitudinal and lateral ecological connectivity. To simulate this, we first drew a digital map that enabled regrouping along the river, where possible, all grassland fields (i.e. meadows and pastures) scattered throughout the plain so as to constitute the buffer habitat matrix. Second, we selected emblematic, endangered species of local biomes, defined their ecological requirements (habitat patch size and connectivity for dispersal) and designed a spatial arrangement of their microhabitats that would enable their conjunct coexistence all along the buffer zone. More specifically, we tried to address the following issues: (i) how can one optimize land improvement measures that accompany river restoration for ameliorating conditions for biodiversity?; (ii) which typical local elements of biodiversity should be targeted in priority by restoration?; (iii) what species-specific ecological requirements do these species have?; (iv) how can we recreate habitats fulfilling the requirements of these target species?; and (v) how to arrange these habitats in space from a multi-species perspective? An additional question arose by the fact that such a stretch along a river is longitudinal in essence, while connectivity indices and measures are mostly considering isotropic configurations by metapopulation dynamics conceptual frameworks (Hanski & Thomas 1994; Hanski 1999; Prugh 2009). This could lead to wrong assumptions in terms of species persistence in a longitudinal configuration, notably because species dispersal may operate differently. Therefore, further tests were conducted to see whether there are major differences between an isotropic and longitudinal configuration, which would imply different spatial constraints for planning valuable habitats for biodiversity.

Material and Methods

Study site

The modelling was done along a stretch of the Rhône River between the cities of Sierre and Martigny (Valais, SW Switzerland; 46°19′ N; 7°27′ E). We focused on the sole floodplain, from the river to the foothill contact line (according to the criteria of the Swiss Federal Office for Agriculture), on an area of ca 107.5 km^2. The valley bottom is devoted primarily to agriculture (50% of the study area), notably fruit tree plantations, grasslands and vineyards, interspersed with human settlements, which tend to sprawl, with their commercial belts and industrial estates (Fig. 2). A railway and a highway also run along the valley axis, sometimes immediately adjacent to the river.

GIS-modelling of the buffer zone

For spatial modelling and simulations, QGIS 2.18 was used (Quantum-GIS-Development-Team 2017), relying on a shape-file of the land use, restricted to the sole plain, among the 17 political communities of the study area, as provided by the cantonal authorities (Canton of Valais, 2017). The community of Grône does not have any agricultural land on the plain and had therefore to be excluded from the analysis. The total areas of overall grasslands and of biodiversity promoting area [BPA] grasslands were calculated both per community and by pooling all the 16 communities together. With the help of Google Maps, we assessed where along the foreseen (revitalized) riverbed a biodiversity-friendly grassland buffer zone could be planned, restricting the area to the farmland zone, i.e. excluding sealed areas and those stretches of the Rhône where the railway and highway were directly adjacent to the river. The lengths of the stretches available for creating a biodiversity buffer were measured in GIS. In order to estimate the width of a possible buffer zone along the Rhône, the sum of the grassland areas of each community was divided by the length of the stretch along its stretch of the Rhône. Given these circumstances three communities provide no room for a biodiversity buffer: Chippis area is totally impervious, Charrat territory does not touch the river, while Saxon harbours a highway all along its stretch of the Rhône. Notwithstanding, their grassland availability was still accounted for equally distributing the biodiversity buffer along the Rhône throughout the study area, in a sort of theoretical exercise.

Target species

The target species were first pre-selected based on expert knowledge of local ecological and environmental conditions, considering the possible habitats that could be realistically created within the grassy buffer zone. Only species enlisted in the Swiss list of national priority species (FOEN 2010) were taken into account. Concerning species-specific habitat requirements and dispersal abilities, a literature search was conducted in Web of Science and Google Scholar. Precedence was given to peer-reviewed literature.

R-function for model comparison

All analysis were done in R studio with R 3.2.4 (R-Core-Team 2016). To compare longitudinal and isotropic configurations, Hanski's metapopulation model

$$S_i = \sum_{j \neq i} \exp\left(-\alpha d_{ij}\right) A_j \qquad \text{Equation 1}$$

(Hanski 1994; Hanski 1999; Hanski & Ovaskainen 2000) was applied to our two configurations (longitudinal vs isotropic). The model can be expressed by a matrix M consisting of

$$m_{ij} = \exp\left(-\alpha d_{ij}\right) A_i A_j \,, \quad for\ j \neq i\ and\ m_{ii} = 0, \qquad \text{Equation 2}$$

with $1/\alpha$ being the average dispersal distance, d_{ij} the distance of patch i to patch j, A_i the area of patch i and A_j the area of patch j. The leading eigenvalue of this matrix λ_M is the metapopulation capacity of a fragmented landscape (Hanski & Ovaskainen 2000). A species can persist if, and only if $\lambda_M > \frac{E}{C}$ where E is the extinction rate and C the colonization rate of the species in the landscape. The matrix was formulated into a function in R, which yields as output whether a species is able to persist in the landscape (Appendix 1). To account for different options of microhabitat configuration (longitudinal vs isotropic), the distance matrix was adapted from a hexagonal grid in the isotropic configuration to a line in the longitudinal configuration. As extinction and colonization coefficients are mostly unknown for our target species and furthermore difficult to estimate, both were set to a value of 1. Metapopulation persistence was then calculated for target species-specific habitat patch sizes and inter-patch distances and visualised graphically. Different scenarios were simulated. In every scenario, the same range of habitat patch sizes (10-1000 m^2) and distances to the nearest neighbouring patch (100-5000 m) was tested, with different widths of the buffer zone (50 and 200 m, respectively), available area (238 and 943 ha, for the BPA grasslands only and all grasslands pooled together, respectively) and various average dispersal capacities (50, 100, 150, 200, 250, 300, 500 m).

Results

GIS-modelling of the buffer zone

There were six different types of agricultural land use in the study area: biodiversity promoting area (BPA) grassland (7% of the farmed area), other grassland (18%), arable land (6%), fruit tree plantation (33%), vineyard (26%), vegetable & berry culture (5%), other BPA (2%) and other culture (3%) (Fig. 2). Only the first two categories were retained for calculating the area theoretically available for constituting the buffer zone, resulting in 237 ha of BPA grassland only and 943 ha of general grasslands (the latter including these 237 ha of BPA). The total length of the theoretical biodiversity-friendly grassland buffer (after removing sealed areas and infrastructures) would amount to 21.7 and 25.3 km, along the southern and northern Rhône banks, respectively, stretching along 46.5% of the study area river line. Because grassland availability varied a lot between political communities (16 communities with a total of 999 BPA grasslands and 2805 other grasslands, the width of the potentially resulting buffer zone was extremely heterogeneous (Table 1, Fig. 3), ranging from 6 m (Leytron) up to more than 1’700 m (Martigny). The grasslands had thus, for the purpose of our modelling exercise, to be reshuffled across communities, yielding a buffer zone of 50 m or 200 m, respectively, depending on whether only BPA grasslands or all grasslands were considered (Fig. 4). Whatever the retained above width scenario, such a buffer offers excellent conditions for restoring longitudinal connectivity along the considered Rhône stretch. There are two major unavoidable gaps, however: the eastern gap is due to the highway running immediately alongside the Rhône and the presence a golf course, while the western gap is created by the city of Sion, the chieftown of Valais.

Target species

The matrix of the resulting, biodiversity-friendly buffer zone would optimally consist of those spatially re-allocated grasslands, in which species-specific microhabitats would be created for target species. On the slopes of the embankments, invertebrate-rich xeric grasslands would prosper, which would provide optimal conditions for locally rare and emblematic species. There, the Western green lizard (*Lacerta bilineata*) could coexist next to the Bladder-senna bush (*Colutea arborescens*) that hosts the rare butterfly Iolas blue (*Iolana iolas*), providing that stone and/or trunk piles and patches of bare ground are available. On the plain section of the buffer, which offers cooler and wetter conditions, tall isolated trees would provide habitat for the Scops owl (*Otus scops*) and the Woodchat shrike

(*Lanius senator*), while small- to middle-sized ponds of different size and depth would offer optimal conditions for semi-aquatic species such as the Common (*Bufo bufo*) and the Yellow-bellied (*Bombina variegata*) toads. This information has been visualised in two graphical representations (Fig. 5). See also Appendix 2 for further information on detailed landscape designing according to the habitat requirements of the target species.

The ecological requirements of these different target species in terms of habitat patch size and dispersal potential are summarized in Table 2. Note that for the birds the dispersal capacity plays no role within our regional system. On that base, we can define patterns of spatial recurrence of these microhabitat structures that would guarantee the persistence of healthy metapopulations.

R-Function for model comparison

There was a slight difference between the isotropic and longitudinal models regarding metapopulation persistence: the isotropic performed better than the elongated model under every scenario (Fig. 6, Appendix 3). Yet, these differences remain small at the tested scales, mostly below 10%. Let's illustrate this with an example: a hypothetical model species A that has an average dispersal distance of 150 m for extinction and colonization parameters set to 1. In an isotropic spatial configuration, this hypothetical species would persist with a habitat patch size of 400 m^2 when patches are approximately 2'250 m distant. In contrast, the species persistence in a longitudinal configuration would be 10% less, resulting in a maximum inter-patch distance of 2'000 m (Fig. 6b). Generally, the higher the average dispersal rates, the smaller the differences between the two models. Only at a very low average dispersal distance the difference becomes higher than 10%

(50 m, Appendix 3). None of the target species in this study shows an average dispersal distance lower than 200 m (Table 2), so that it can be assumed that such difference can be considered negligible in the context of the Rhône river. Our simulations further suggest that above a dispersal distance of 500 m the colonisation potential of a suitable habitat patch across a non-hostile grassy matrix is guaranteed in all cases.

Discussion

This study shows that the land improvement operations that typically accompany major river restoration programmes may be instrumental in reallocating the biodiversity-most-supporting farmland habitat (e.g. extensively-managed grasslands) along rivers for reinstating the longitudinal and lateral ecological connectivity that nowadays crudely lacks in corrected streams. By associating to a grassland matrix natural and semi-natural key microhabitat structures that can promote locally rare, emblematic species, general conditions for biodiversity could be greatly enhanced. Our analysis also suggests that land improvement measures should be integrated into the cantonal country-planning master, i.e. beyond local community boundaries across the region, so as to obtain a homogeneous buffer strip all along the river.

As generally acknowledged, such buffer zones around water bodies are important, not only for water protection but also for biodiversity maintenance (e.g. Rudolph & Dickson 1990; Semlitsch & Bodie 2003; Marty *et al.* 2005). In the study area, such a grassy biodiversity-friendly buffer zone could be implemented along almost half of the modelled Rhône river stretch, which would, firstly, drastically increase its longitudinal connectivity compared to the dramatic current ecological situation. Revitalized this way, the Rhône would be likely to become again a functional ecosystem (Ward, Tockner & Schiemer 1999). Secondly, the foreseen microhabitats to be regularly created within the grassy buffer zone for our array of target species would also dramatically enhance their conservation status regionally, since they have mostly vanished following habitat degradation and destruction by agricultural rationalisation (Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2005; Vickery & Arlettaz 2012). It is important to recognize, however, that only a combination of a non-hostile (here grassy) matrix with targeted species-specific microhabitat structures is able to improve conditions for biodiversity in such a system. In effect, the grassy matrix operates as a fluid green corridor, easing dispersal movements, whereas the natural structures (piles of dead wood and stones, bushes, etc.) contribute to create a rich mosaic while offering stepping stones for habitat colonisation, which appears especially crucial for biodiversity persistence within otherwise intensively used landscapes (e.g. Janin *et al.* 2009). If managed extensively, the grassy buffer matrix will not only increase landscape permeability for terrestrial biodiversity but also improve foraging conditions overall (Ray, Lehmann & Joly 2002; Janin *et al.* 2009; Salazar *et al.* 2016). Finally, the spatial recurrence pattern of the dedicated microhabitats will be key to reinstate full ecosystem functions (Prevedello & Vieira 2010; Ruffell, Clout & Didham 2017). As such, larger gaps should always be within the maximal dispersal distance of an organism to allow metapopulation viability.

Contrary to scientific information about habitat patch size requirements and dispersal distance of our target species, we found no quantitative data about their specific extinction-colonization dynamics. Hence, the parameters used in our metapopulation simulations had to be set to 1. The limit of our approach is therefore that it is purely theoretical. Notwithstanding, the simulations show that a species facing an isotropic habitat configuration has a higher probability of persistence in a landscape than in an elongated environment, which is well supported by empiric data (e.g. Petren & Case 1998; Kerr, Southwood & Cihlar 2001; Rahbek & Graves 2001; Johnson *et al.* 2003). However, this slight difference remains negligible from a landscape designing viewpoint. More important, in contrast, is the spatial pattern of recurrence of the microhabitats within the grassy buffer matrix, which must be defined based on species' dispersal ability. The simulation trade-offs observed between habitat patch size and inter-patch distance indicate that species with sufficient dispersal power will have no problem to colonise suitable habitat patches: above a dispersal capacity of 500 m and in presence of a non-hostile matrix such as extensively-managed grasslands, no obstacles seem to hamper habitat colonisation. We are confident that terrestrially-dispersing species among our targets, and by extension any species that could be associated with them and profit from the same microhabitats, would be able to effectively move across the matrix to reach suitable habitat patches. The illustrations of habitat configurations provided here (Fig. 5) can therefore serve as a reference basis for practitioners, while Appendix 2 provides further details about aspects to consider for creating a suitable series of microhabitats for the target species and beyond.

In the specific case of the third Rhône correction, in addition to a riverbed widening by a factor 1.5–1.6, the authorities foresee a few major larger broadenings of the bed along a few stretches, up to a factor of 2–3 (Rey 2014). If those can favour later stages of the habitat and vegetation succession, which cannot be met with the smaller widenings, they will in any case not be sufficient to restore integral ecological connectivity, which calls for additional measures that can only be implemented outside the levees, where land allows (neither settlements nor heavy infrastructure). This is precisely what is proposed in this study, by regrouping along the river the numerous grasslands scattered on the plain in order to constitute a continuous and functional ecological buffer. This buffer will be an integral part of the farmed area, i.e. in any case not subtracted from agricultural exploitation. It may also facilitate farmers work by rationalising the logistics for fodder production and grazing activities (Haug, Züblin & Schmid 2011; Oeschger 2011). At present, in effect, the grassland fields are fairly small and scattered all over the floodplain.

Clearly, however, only a collective approach involving all regional farmers and stakeholders would guarantee successful implementation (Naiman, Decamps & Pollock 1993; Arlettaz *et al.* 2010; Knaus *et al.* 2016). As resistance to such a major spatial (and mental) paradigmatic shift is to be expected, efficient steering supervision by the political authorities and the administration in charge of town and country planning are an absolute requisite.

Note that our projections are based on two scenarios (all grasslands or only BPA grasslands spatially reallocated). In case of massive resistance or will to maintain grasslands elsewhere on the plain, a solution would be to reallocate along the Rhône only a fraction of the grasslands, preferably the BPA grasslands. From this viewpoint, we have to stress that only the grasslands occurring on the plain (flat land) were considered here, meaning we did not include the grasslands on the adjacent foothills.

In addition to improve accessibility and logistics for farmers, benefits would of course also arise for biodiversity, with enhanced metapopulation dynamic functionalities due to a spatial aggregation of the most valuable farmland habitats next to the revitalised river, with the two together creating an outstanding dual green corridor. Hence, in addition to some lateral (grassy-riparian-riverine habitat) connectivity, it is principally the longitudinal connectivity that will mostly profit from those massive structural changes. Former studies have already pointed out that river-wide efforts should be preferred to local, site-specific measures where possible to enhance the longitudinal connectivity (Naiman, Decamps & Pollock 1993).

In the context of the Rhône river, two unavoidable gaps in longitudinal connectivity were identified, due mainly to urbanisation (Fig. 3 and 4). The eastern gap might probably be somehow bypassed as it consists of a nature reserve and a golf course that can probably serve as stepping stones for dispersal of some terrestrial species (Tanner & Gange 2005), but the western is a fully sealed, high-density urban area where the riverbed cannot even be broadened. Bypassing this major gap might necessitate the translocation of the less mobile organisms, at least in an initial phase following habitat creation (Schmidt & Zumbach 2008).

However, another obstacle to (lateral) dispersal, notably for fairly sedentary terrestrial organisms might be the river itself (Hayes & Sewlal 2004; Li *et al.* 2009). It was not considered a gap in our projections because relict populations of most target species currently occur on both sides of the Rhône, but some associated elements of strictly terrestrial biodiversity may experience it as a major resistance to dispersal. Since the maximal dispersal distances of the target species are all larger than 1 km (Table 2), we consider the issue of this lateral spatial gap as secondary.

One major conclusion of this study is that land improvement operations, if carried out in full consideration of ecological integration, can provide decisive instruments for conserving and restoring biodiversity, as exemplified here with the third Rhône correction project. As such, they offer valuable tools for designing the multi-functional ecosystems of the future. However, an excellent knowledge of local ecological communities, including fine-grained species-habitat associations, complemented as far as possible with information about species habitat patch size requirements and dispersal potential, is prerequisite to any such exercise of landscape designing. This study provides a general conceptual framework for major river restoration projects in constrained environments and a detailed vision, accompanied by clear habitat creation targets, for what could be the Rhône landscape of the future.

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Tables

Table 1. Grassland area (biodiversity promoting area grasslands and total grasslands), length of available Rhône stretch and potential width of the respective potential buffer zone per community, in alphabetic order.

Community	BPA grassland area [m2]	Total grassland area [m^2]	Length of available Rhône [m]	BPA grassland buffer [m]	Total grassland buffer [m]
Ardon	125’642	272‘405	1‘533	82	178
Chamoson	64’854	130‘414	4‘322	15	30
Charrat	144’920	479‘424	0	-	-
Chippis	13’054	18‘893	0	-	-
Conthey	57’722	163‘119	802	72	203
Fully	204’426	404‘172	9’683	21	42
Leytron	9’983	95’904	1’754	6	55
Martigny	670’547	2’106’927	1’232	544	1’710
Nendaz	25’667	119’413	2’433	11	49
Riddes	38’679	238’641	4’464	9	53
Saillon	136’115	397’837	4’267	32	93
Saxon	112’258	276’540	0	-	-
Sierre	218’816	1’113’560	6’275	35	177
Sion	395’049	2’496’379	7’427	53	336
St. Léonard	35’966	406’364	1’224	29	332
Vétroz	126’051	709’888	1’759	72	404
Total	2’379’749	9’429’880	47’175	50	200

Table 2. Target species, their habitat requirements and dispersal abilities.

Species	Structural element	Area of territory	Maximum dispersal distance	Source
Western green lizard (*Lacerta bilineata*)	Piles of stones or deadwood (ca. 5 m^3) every 200 m	4 ha of sun-exposed grassland for sustaining a population (*Lacerta viridis* in Germany)	4 km (*Lacerta viridis* in Germany)	Sound & Veith 2000; Guisan & Hofer 2003, Bohme *et al.* 2007; KARCH 2011
Iolas blue (*Iolana iolas*)	20 *Colutea arborescens* bushes next to a mineral (bare) ground patch every 550 m	2 ha with various *Colutea arborescens* bush patches	1.5 km	Rabasa, Gutierrez & Escudero 2007; Sierro 2007; Heer *et al.* 2013
Scops owl (*Otus scops*)	Tall trees with cavities or nest boxes every 350 m	10 ha grassland per pair, rich in bush crickets	no barrier: flies	Glutz von Boltzheim & Bauer 1980; Arlettaz 1990
Woodchat shrike (*Lanius senator*)	Groups of 3-10 high trunk fruit trees every 500 m	8 ha of insect-rich grassland per pair	no barrier: flies	Glutz von Boltzheim & Bauer 1993
Common toad (*Bufo bufo*)	Permanent ponds deeper than 50 cm every 300 m	5 ha terrestrial habitat around pond, close to woody habitat	3 km	Reading, Loman & Madsen 1991; Hartel & von Wehrden 2013
Yellow-bellied toad (*Bombina variegata*)	Small temporary ponds (<20 m^2) less deep than 100 cm that dry out occasionally, every 200 m	5 ha good terrestrial habitat around pond to provide prey, close to woody vegetation	1 km	Beshkov & Jameson 1980; Hartel 2008; Hartel & von Wehrden 2013

Figures

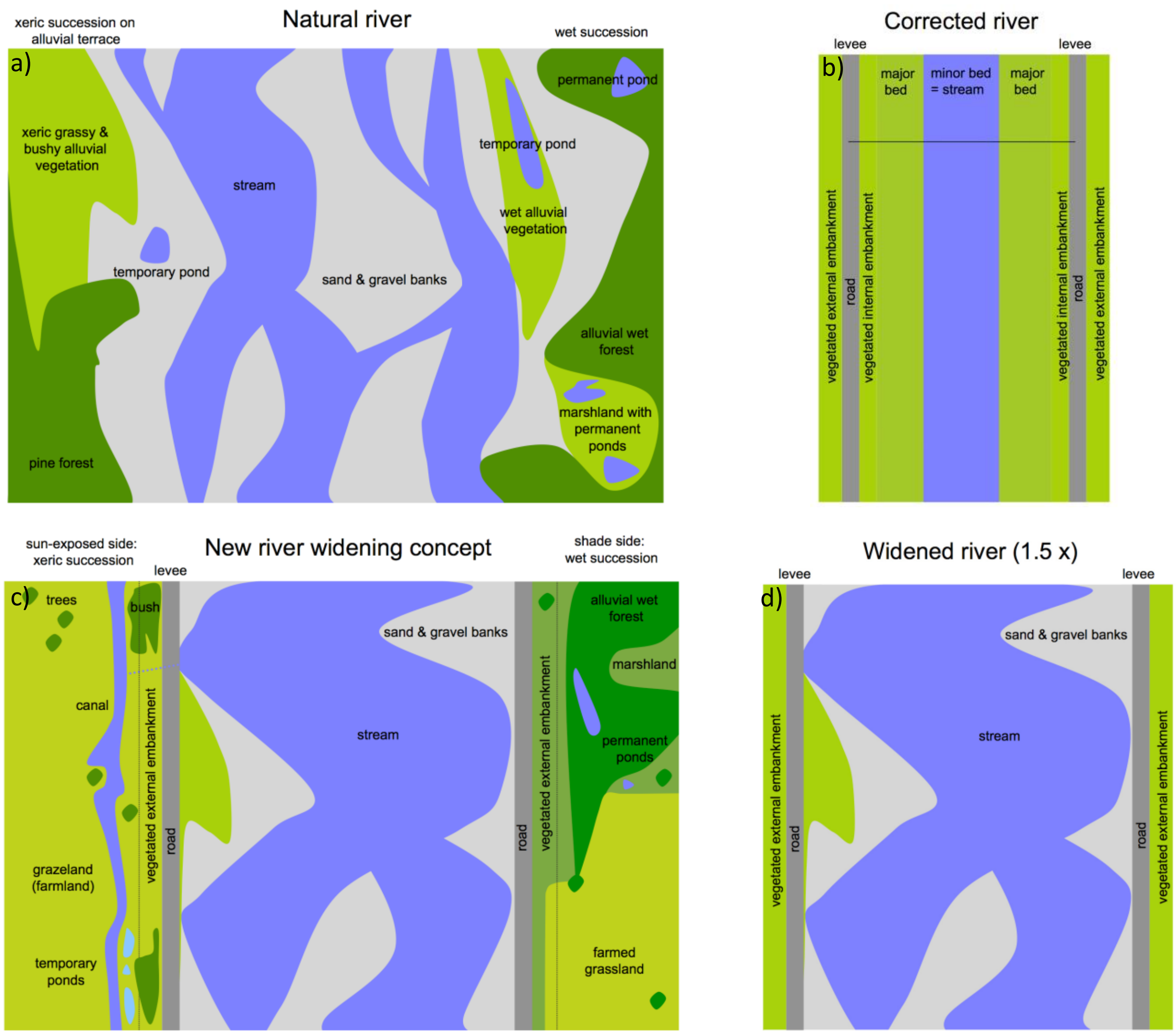

Figure 1. Own schematic representation of (a) a natural river, (b) a conventionally corrected river, (c) a river widened by a factor 1.5 with additional buffer zones outside the levees, (d) a river restored with today's standard of widening the bed by a factor 1.5 without a buffer zone. C illustrates the integrated concept of river restoration developed in this study.

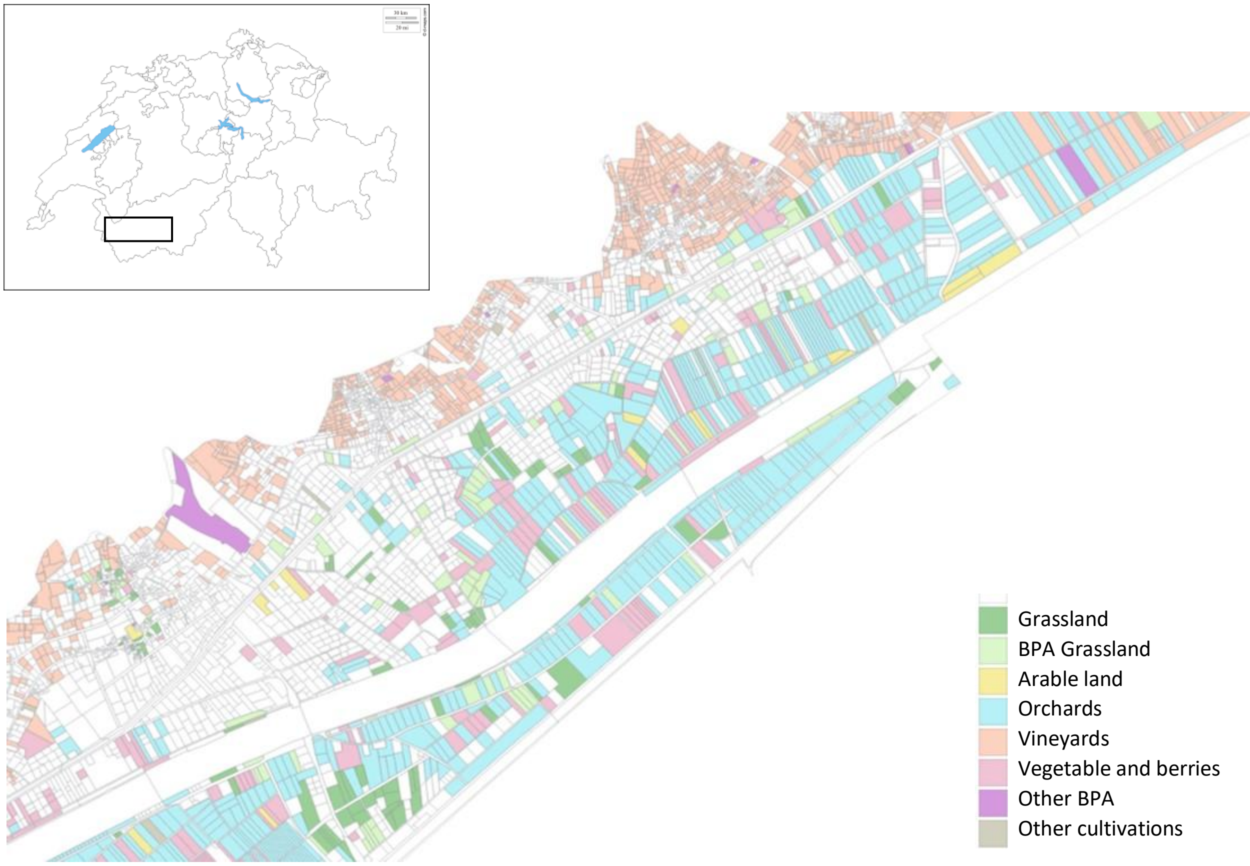

Figure 2. A section of the alluvial plain in our study area (Fully, Valais, SW Switzerland) showing the scatter of the different agricultural types, notably that of grasslands. Regrouping these grasslands along the Rhône in a buffer zone would not only promote biodiversity but also contribute to rationalise the exploitation of hay meadows and pastures.

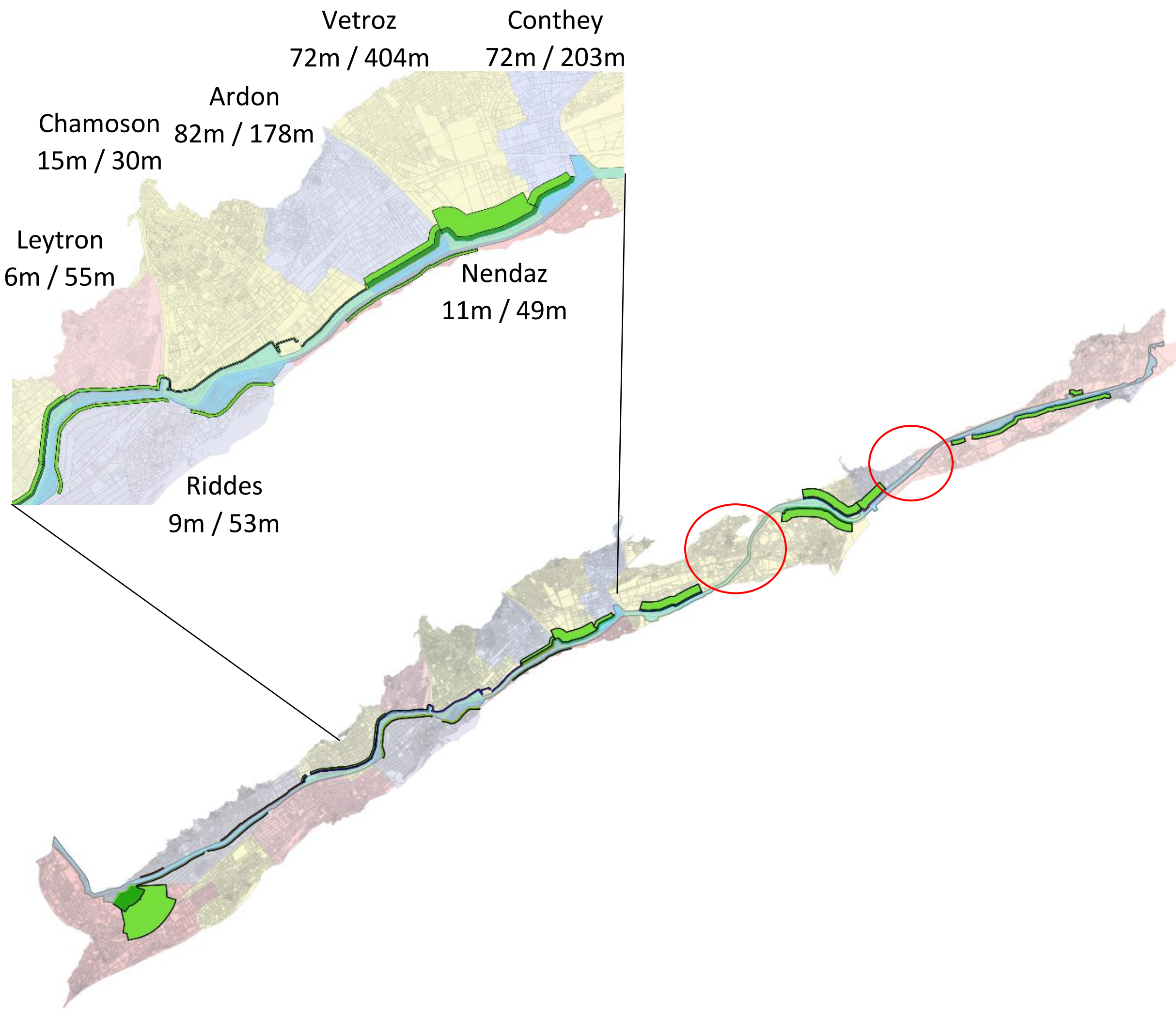

Figure 3. Potential buffer zones (BPA grassland or all grasslands together, respectively) resulting from redistribution along the Rhône of the grasslands available per community (the excerpt shows it in more detail). A community-level approach delivers very heterogeneous widths of buffer zones and strips along the studied river stretch, which is not optimal for both lateral and longitudinal ecological connectivity, without mentioning agricultural purposes. Major connectivity gaps (> 2 km) due to human settlements and infrastructures are indicated by the two red circles.

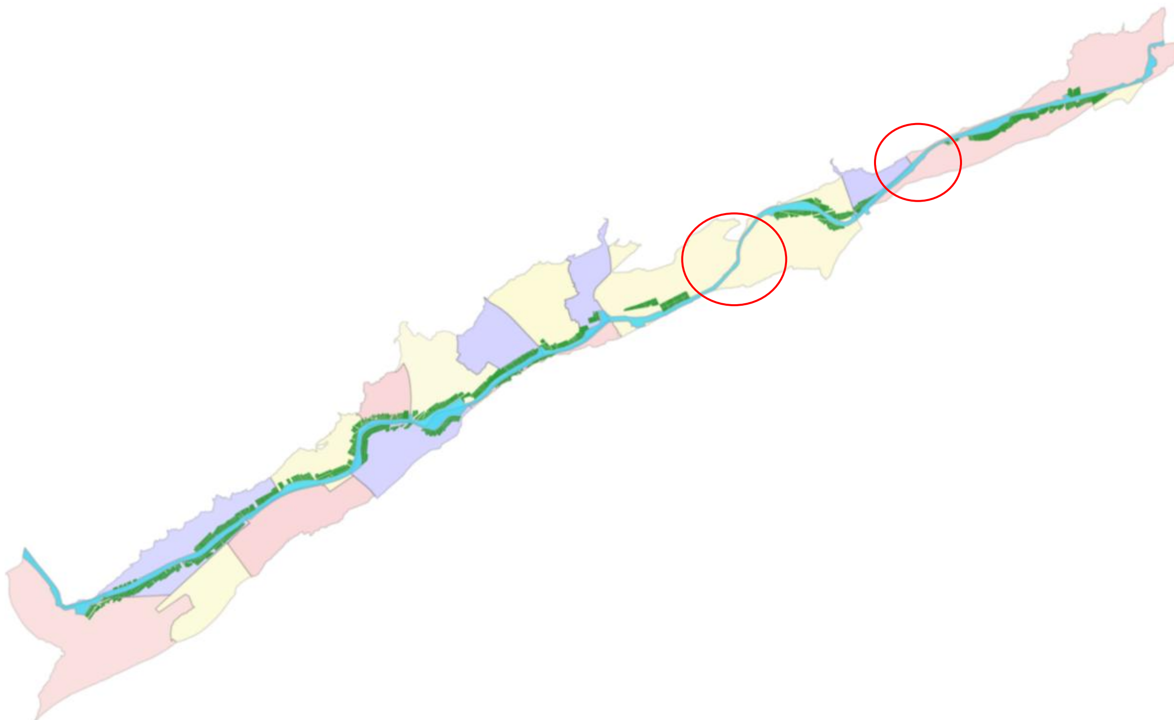

Figure 4. Potential buffer zones (200 m broad) resulting from a redistribution along the Rhône of all the grasslands available across the study area, pooling the different communities. A regional approach delivers a homogeneous buffer zone that would contribute to restore both lateral and longitudinal ecological connectivity. Note the two major residual connectivity gaps (> 2 km), due to human settlements and infrastructures, that cannot be eliminated (red circles).

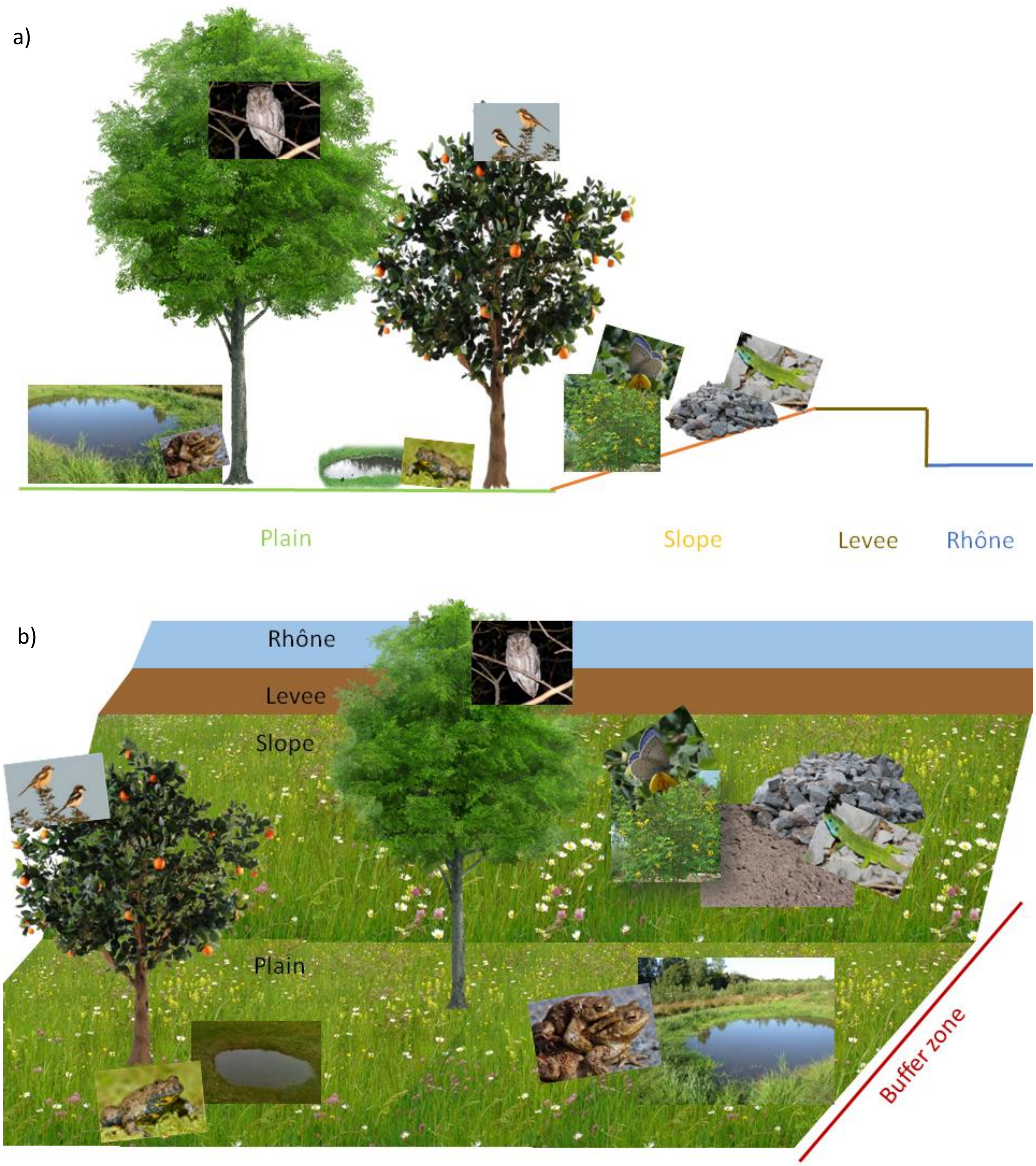

Figure 5. Schematic representations of the potential buffer zone along the Rhône river with the target species and their required microhabitats in an extensively managed grassland matrix.

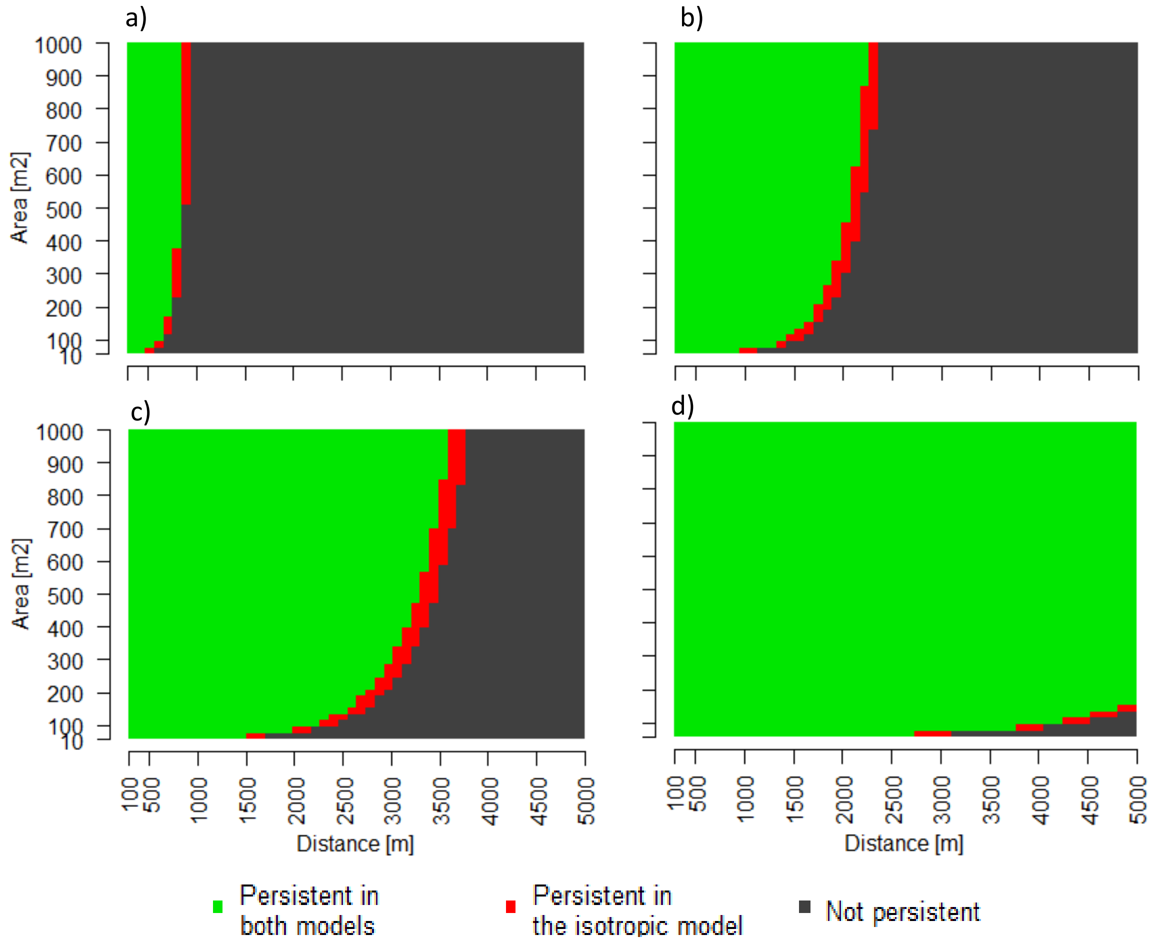

Figure 6. Differences between meta-population persistence of target species under an isotropic vs longitudinal configuration of the grassy buffer zone. We focused on the sole BPA grasslands (237 ha in total) for conducting these simulations, using a constant buffer width of 50 m, but varying dispersal distance: a) 50 m, b) 150 m, c) 250 m and d) 500 m. The two spatial configurations show only tiny differences, whereas dispersal capacity is key, which calls for a regular spatial recurrence of key target species microhabitats all along the buffer strip.

Appendix

Appendix 1. R-Code

```
## Parameters: ----
# Areas      # Areas of the Patches [m2]
# Distances  # Distances between 2 Patches [m]
# avmd       # Average migration distance [m]
# ha         # how many hectares is the whole Area [ha]
# width      # how wide is the Buffer zone [m]
# ex; co     # Extinction and Colonisation rate estimates (1 is default in function)


## Fucntion for Longitudinal Model: ----
MM_long = function(Areas, Distances, avmd, ha, width, ex = 1, co = 1) {

  l = ha*10000/width           # length of whole Area [m]

  # alpha
  alpha = 1/avmd
  #

  z = 1
  lambda = numeric()
  for(id in 1:length(Distances)){

    for(ia in 1:length(Areas)){
      # d_ij
      dia = 2*sqrt(Areas[ia]/pi)     # average diameter of patches [m] (Kreisberechnung)
      annex = Distances[id]+dia      # one annex
      nr = round(l/annex)            # nr = number of patches that fit in the stretch,
                                     # as you have from the beginning ann you have left and right a buffer from the edge
      if (nr<2) {
        stop("Number of patches in one scenario less than 2")
      }
      x.crd = round(seq(from = 0, by = annex, length.out = nr)) # set the distances for the szenario (from 0 on nr times Distances
further)
      d1 = as.matrix(dist(x.crd))                               # distance matrix for d_ij
      #

      # A_i, A_j
      A = rep.int(x = Areas[ia], times = nr+1)   # set an area for the patches (as per szenario they are all the same, just repeat
the area nr+1 times) for A_i and A_j
      #
```

```
      # M resp. m_ij
      m1 = matrix(NA, nrow = nr, ncol = nr)              # Matrix for one szenario
      for(i in 1:nr){                                   #       "
        for(j in 1:nr){                                 #       "
          m1[i,j] = exp(-alpha*d1[i,j])*A[i]*A[j]       #       " (Formula for m from Hanski_Oikos1999)
        }                                              #       "
      }                                                #       "
      diag(m1) = 0                                     # so i!=j
      #

      # lambda_M
      lambda[z] = max(eigen(m1)$values)                 # get the max. eigenvalue of the matrix and save it in "lambda",
      #

      z = z+1                                          # so you have the lambda for this szenario
      # Now get to the new szenario with a different Area
    }

  }

  lambda_matrix = matrix(lambda, ncol = length(Areas) ,       # get the lamdas in a matrix form
                         byrow = T, dimnames = list(Distances, Areas))


  delta = ex/co
  Persist = ifelse(test = lambda_matrix > delta, yes = 1, no = 0)   # Test if Population persists in the different scenarios
  # (lambda > e/c, Hanski_Oikos1999 eq.13)
  return(Persist)
}

## Function for isotropic Model -----
MM_iso = function(Areas, Distances, avmd, ha, width, ex = 1, co = 1) {

  # alpha
  alpha = 1/avmd
  #

  # get the same amount of patches as in longitudinal
  l = ha*10000/width           # length of whole Area [m]
  z = 1
  lambda2 = numeric()

  for(id in 1:length(Distances)){
```

```
    for(ia in 1:length(Areas)){
      dia = 2*sqrt(Areas[ia]/pi)      # average diameter of patches [m]
      annex = Distances[id]+dia       # one annex in longitudinal
      nr = round(l/annex)             # nr = number of patches (that fit in the longitudinal)

      if (nr<2) {
        stop("Number of patches in one scenario less than 2")
      }
      #

      # distance matrix resp. d_ij
      li = 0                       # Lines apart
      M = list()                   # List of matrices
      x = ceiling(sqrt(nr))        # number of points in (horizontal) direction
      for(h in 1:x){
        m = matrix(NA, nrow = x+1, ncol= x+1)
        p=0
        for(i in 1:(x+1)){
          q=p
          for(j in 1:(x+1)){
            m[i,j]   =   round(sqrt((li*Distances[id])^2   +   (q*Distances[id])^2   -   (2*(li*Distances[id])*(q*Distances[id])   *
cos(pi/3))))
            q=q+1
          }
          p=p-1
        }
        M[[h]] = m
        li = li+1
      }
      index <- seq_along(M)
      Final = do.call(rbind, lapply(index, function(i) do.call(cbind, M[abs(i-index)+1]))) #
      d2 = as.matrix(Final[1:nr,1:nr] )                           # cut the matrix to the nr of plots
      #

      # A_i, A_j
      A  =  rep.int(x  =  Areas[ia],  times  =  nr+1)    #  set  an  area  for  the  szenario  (as  per  szenario  they  are  all  the  same,  just
repeat the area nr+1 times)
      #

      # M resp. m_ij
      m2 = matrix(NA, nrow = nr, ncol = nr)            # Matrix for one szenario
      for(i in 1:nr){                                 #       "
        for(j in 1:nr){                               #       "
          m2[i,j] = exp(-alpha*d2[i,j])*A[i]*A[j]     #       " (Formula for m from Hanski_Oikos1999)
```

```
        }                                                 #       "
      }                                                   #       "
      diag(m2) = 0                                        # so i!=j
      #

      # lambda_M
      lambda2[z] = abs(eigen(m2)$values[1])            # get the max. eigenvalue ([1]) of the matrix (abs() because it has complex
numbers) and save it in "lambda",
      #

      z = z+1                                             # so you have the lambda for this szenario
      # Now get to the new szenario with a different Area
    }

  }

  lambda_matrix2 = matrix(lambda2, ncol = length(Areas) ,       # get the lamdas in a matrix form
                          byrow = T, dimnames = list(Distances, Areas))


  delta = ex/co
  Persist2 = ifelse(test = lambda_matrix2 > delta, yes = 1, no = 0)   # Test if Population persists in the different scenarios
  # (lambda > e/c, Hanski_Oikos1999 eq.13)
  return(Persist2)
}

## Percentage difference between the two models ----
Diff_percent = function(Iso, Long) {
  r_long = numeric()
  for(i in 1:ncol(Long)){
    if(sum(Long[,i]) == nrow(Long)){
      r_long[i] = as.numeric(rownames(Long)[nrow(Long)])
    } else {
      r_long[i] = as.numeric(rownames(Long)[(as.numeric(min(which(Long[,i] == 0)))-1)])
    }
  }

  r_iso = numeric()
  for(i in 1:ncol(Iso)){
    if(sum(Iso[,i]) == nrow(Iso)){
      r_iso[i] = as.numeric(rownames(Iso)[nrow(Iso)])
    } else {
      r_iso[i] = as.numeric(rownames(Iso)[(as.numeric(min(which(Iso[,i] == 0)))-1)])
    }
```

```
  }

  difference_absolute = r_iso - r_long
  difference_percent = round((100/r_iso*r_long)-100, digits = 2)    # r_iso = 100% -> how much % less is r_long
  # difference = list("absolute" = difference_absolute, "percent" = difference_percent)    # return this to get both
  return(difference_percent)
}

## Function for graph ----
G = function(Iso, Long, Areas, Distances, ha, w){
  par(mar = c(6,4,2,1))
  image(1:nrow(Iso), 1:ncol(Iso), as.matrix(Iso), col=c(rgb(0,0,0, alpha = 0.75), rgb(1,0,0, alpha = 1)),
        xlab = "Distance [m]", ylab = "Area [m2]", xaxs = "r", yaxs = "r", axes = F)
  par(new = T)
  image(1:nrow(Long), 1:ncol(Long), as.matrix(Long), col=c(rgb(0,0,0, alpha = 0), rgb(0,0.9,0, alpha = 1)),  xlab = "", ylab = "",
        xaxs = "r", yaxs = "r", axes = F)

  labels_D = round(seq(from = 0, to = D[length(D)], length.out = 11))
  labels_D[1] = D[1]
  axis(side = 1, at = c(0, nrow(Long)/(length(labels_D)*2))+0.5, labels = c(labels_D[1], ""), las = 2) # the first tick
  axis(side = 1, at = seq(from = nrow(Long)/(length(labels_D)*2), to = nrow(Long), length.out = length(labels_D)-1)+0.5,
       labels = labels_D[-1], las = 2) # the other ticks

  labels_A = round(seq(from = 0, to = A[length(A)], length.out = 11))
  labels_A[1] = A[1]
  axis(side = 2, at = c(0, ncol(Long)/(length(labels_A)*2))+0.5, labels = c(labels_A[1],""), las = 1) # the first tick
  axis(side = 2, at = seq(from = ncol(Long)/(length(labels_A)*2), to = ncol(Long), length.out = length(labels_A)-1)+0.5,
       labels = labels_A[-1], las = 1) # the other ticks

  mtext(text = paste(ha, "ha total area, ", w, "m width of buffer zone, ", avmd, "m average migration rate", sep = ""),
        side = 3, line = 0, cex = 0.7)

  par(fig = c(0, 1, 0, 1), oma = c(0, 0, 0, 0), mar = c(0, 0, 0, 0), new = TRUE)
  plot(0, 0, type = "n", bty = "n", xaxt = "n", yaxt = "n")
  legend(x = "bottom", legend = c("Persistent in \nboth models", "Persistent in \nthe isotropic model     ", "Not persistent"),
         xpd = TRUE, horiz = TRUE, bty = "n", pch = 15, cex = 0.8,
         col = c(rgb(0,0.9,0, alpha = 1), rgb(1,0,0, alpha = 1), rgb(0,0,0, alpha = 0.75)))
}
```

Appendix 2. Detailed habitat requirements of the target species.

In addition to the grassy matrix, the microhabitats to be created for our target species will constitute a rich mosaic that will benefit many other elements of biodiversity. This is because all these species are enlisted as national priority species (FOEN 2010) for which specific conservation measures have to be implemented, meaning they are likely to play the role of umbrellas for entire ecological communities. The grassland matrix should be managed extensively (BPA hay meadows, high quality pastures, etc.) to harbour diverse invertebrate communities and abundant populations, which will provide good food supplies for insectivorous species such as the (locally extinct but migratory) Woodchat shrike or the Scops owl (which specialises on bush crickets; Arlettaz *et al.* 1990). The Woodchat shrike requires tall trees, if possible high trunk fruit trees, as nest sites (Glutz von Blotzheim & Bauer 1993). Once mature, these fruit trees and other tall deciduous trees will provide cavities, natural or excavated by woodpeckers, offering nesting opportunities for secondary cavity breeders such as the Scops owl. Before trees reach maturation, however, nest boxes could temporary offer some suitable breeding sites.

Amphibians might have higher ecological demands to support viable populations. They are dramatically declining worldwide due to climate change, chemical pollution, new diseases and pathogens, commercial trade, out competition by invasive species, but habitat destruction, alteration and fragmentation represent major threats in Switzerland (e.g. Semlitsch 2000a; Semlitsch 2000b; Cushman 2006; Borgula, Schmidt & Zumbach 2010; Schmidt *et al.* 2015). Amphibians crudely need ponds in the Swiss lowlands, in particular temporary ponds that dry out in late summer or winter, which eliminates fish and other insects preying on eggs or tadpoles. Species like the Yellow-bellied toad are particularly concerned (Barandun & Reyer 1998; Hartel, Nemes & Mara 2007; Schmidt *et al.* 2015). Other species such as the Common toad tend to prefer deeper, permanent ponds, however (Reading, Loman & Madsen 1991). As both species can cover distances up to more than 1 km, ponds of different sizes and depths should be present in the form of a local network and, if possible, not far from structures such stone and wood piles, hedges or even forests that serve as overwintering habitat (Semlitsch 2002). The sun-exposed slopes of the levees will offer the most xeric habitats for reptiles, including the target species Western green lizard. For its habitat requirements, we had to refer to literature on its sister species *Lacerta viridis* from which it was recently split (Rykena 1991). Besides creating deadwood structures and piles of stones, the plantation of groups of bladder-senna bushes (*Colutea arborescens*) for the Iolas blue will also offer good habitat conditions for the green lizard.

Appendix 3. Differences (in %) in inter-habitat patch distances ensuring meta-population persistence between an isotropic vs longitudinal configuration of the buffer zone for different habitat patch sizes (m^2) and dispersal capacities (distances in m). Only the buffer zone obtained from BPA grasslands (50m width, 237 ha) have been used for these simulations. See also Fig. 6.

Patch area [m^2]	Dispersal 50 m	Dispersal 100 m	Dispersal 150 m	Dispersal 200 m	Dispersal 250 m	Dispersal 300 m	Dispersal 500 m
10	-33.33	-16.67	-22.22	-16.67	-13.33	-16.67	-13.33
30	-25.00	-12.50	-8.33	-12.50	-10.00	-8.33	-7.50
50	0.00	-11.11	-14.29	-11.11	-8.70	-7.41	-6.67
71	-20.00	-10.00	-13.33	-10.00	-8.33	-6.90	-6.25
91	-20.00	-10.00	-6.67	-9.52	-7.69	-9.68	-4.00
111	-20.00	-18.18	-6.25	-4.76	-7.41	-6.25	0.00
131	0.00	-9.09	-6.25	-9.09	-7.41	-6.06	0.00
151	0.00	-9.09	-11.76	-4.55	-7.14	-8.82	0.00
172	0.00	-9.09	-5.88	-8.70	-6.90	-5.88	0.00
192	-16.67	-8.33	-11.11	-4.35	-6.90	-5.71	0.00
212	-16.67	-8.33	-11.11	-8.33	-6.67	-8.33	0.00
232	-16.67	-8.33	-5.56	-8.33	-6.67	-5.56	0.00
252	-16.67	-8.33	-5.56	-4.17	-6.45	-5.41	0.00
273	-16.67	-8.33	-10.53	-8.00	-6.45	-5.41	0.00
293	-16.67	-8.33	-10.53	-8.00	-6.45	-5.41	0.00
313	-16.67	-15.38	-5.26	-4.00	-6.25	-5.26	0.00
333	-16.67	-7.69	-5.26	-7.69	-6.25	-5.26	0.00
353	0.00	-7.69	-5.26	-7.69	-6.25	-7.69	0.00
374	0.00	-7.69	-10.00	-7.69	-6.06	-5.13	0.00
394	0.00	-7.69	-10.00	-3.85	-6.06	-5.13	0.00
414	0.00	-7.69	-10.00	-3.85	-6.06	-7.50	0.00
434	0.00	-7.69	-5.00	-7.41	-6.06	-5.00	0.00
454	0.00	-7.69	-5.00	-7.41	-5.88	-5.00	0.00
475	0.00	-7.69	-5.00	-7.41	-5.88	-5.00	0.00
495	-14.29	-7.69	-5.00	-7.41	-5.88	-5.00	0.00
515	-14.29	-14.29	-5.00	-3.70	-5.88	-4.88	0.00
535	-14.29	-14.29	-9.52	-3.70	-5.88	-4.88	0.00
556	-14.29	-7.14	-9.52	-7.14	-2.94	-4.88	0.00

576	-14.29	-7.14	-9.52	-7.14	-5.71	-4.88	0.00
596	-14.29	-7.14	-9.52	-7.14	-5.71	-4.76	0.00
616	-14.29	-7.14	-4.76	-7.14	-5.71	-4.76	0.00
636	-14.29	-7.14	-4.76	-7.14	-5.71	-4.76	0.00
657	-14.29	-7.14	-4.76	-3.57	-5.71	-4.76	0.00
677	-14.29	-7.14	-4.76	-3.57	-5.71	-4.76	0.00
697	-14.29	-7.14	-4.76	-6.90	-5.56	-6.98	0.00
717	-14.29	-7.14	-4.76	-6.90	-5.56	-4.65	0.00
737	-14.29	-7.14	-9.09	-6.90	-5.56	-4.65	0.00
758	-14.29	-7.14	-9.09	-6.90	-5.56	-4.65	0.00
778	-14.29	-7.14	-9.09	-6.90	-5.56	-4.65	0.00
798	-14.29	-7.14	-9.09	-6.90	-5.56	-4.65	0.00
818	-14.29	-7.14	-9.09	-6.90	-5.56	-4.65	0.00
838	-14.29	-13.33	-9.09	-6.90	-8.11	-4.55	0.00
859	-14.29	-13.33	-9.09	-3.45	-5.41	-4.55	0.00
879	-14.29	-13.33	-4.55	-3.45	-5.41	-4.55	0.00
899	-14.29	-13.33	-4.55	-6.67	-5.41	-4.55	0.00
919	-14.29	-13.33	-4.55	-6.67	-5.41	-4.55	0.00
939	-14.29	-6.67	-4.55	-6.67	-5.41	-4.55	0.00
960	-14.29	-6.67	-4.55	-6.67	-5.41	-4.55	0.00
980	-14.29	-6.67	-4.55	-6.67	-5.41	-6.67	0.00
1000	-14.29	-6.67	-4.55	-6.67	-5.41	-4.44	0.00
Mean	-12.46	-9.24	-7.65	-6.90	-6.33	-5.78	-0.76

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname:	Knutti Jasmin Olivia
Matrikelnummer:	12-111-316
Studiengang:	Master of Science in Ecology and Evolution with special qualification in Animal Ecology and Conservation
	Bachelor ☐ Master ☑ Dissertation ☐
Titel der Arbeit:	Reinstating longitudinal ecological connectivity in major river restoration projects: land improvement as a tool to create a biodiversity buffer outside levees
LeiterIn der Arbeit:	Prof. Dr. R. Arelttaz

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.
Ich gewähre hiermit Einsicht in diese Arbeit.

Ort/Datum

Unterschrift