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Improving longitudinal habitat connectivity in major river restoration projects through farmland re-allocation

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A B S T R A C T

River restoration projects are often accompanied by major land consolidation operations, notably the re-allocation of adjacent farmland, which offers the opportunity to create an extensively-managed buffer zone outside the levees where specific habitat features are installed for endangered terrestrial and semi-aquatic biodiversity. Modern, enirivonmentally-friendly land consolidation operations 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 consolidation, we simulated the creation of 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 focal species depending on a palette of complementary habitat features, 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 these habitat features. Since such a buffer zone will necessarily stretch along the riverbed, which implies different spatial contraints and consequential planning strategies, we tested two scenarios via a metapopulation model: (i) arranging key habitat features longitudinally or (ii) positioning them in an isotropic context. Simulations showed that differences in metapopulation connectivity between scenarios were negligible at the foreseen scale. We conclude that land consolidation via targeted farmland re-allocation 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.

1. Introduction

Rivers are key biodiversity hotspots but also among the ecosystems most affected by human activities (Revenga, Brunner, Henninger, Kassem, & Payne, 2000; Vitousek, Mooney, Lubchenco, & Melillo, 1997). 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 infrastructure, from increased flood recurrence, river restoration has 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. Yet, given the spatial constraints in human-dominated landscapes (Gillilan, Boyd, Hoitsma, & Kauffman, 2005), such enlargements are mostly still restricted to a dammed zone and are thus rarely sufficient to fully restore the fluvial processes and allow the re-establishment of natural riparian communities. Under the usually prevailing circumstances, in effect, it is hardly achievable to reconstitute the whole range of riparian habitat types (i.e. the different stages of vegetation succession).

All the more it is important to develop a guiding image for creating riverine and riparian ecosystems under constrained conditions. Complementing natural renaturation processes with the active creation of semi-natural habitats could be one option for providing maximal benefits for biodiversity and ensure the persistence of crucial ecosystem

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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 is 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 refers to 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 rebuilding transitions between various riparian habitats along the river, providing different successional stages and contributing to better integrating the new river into the wider landscape (Ficetola, Padoa-Schioppa, & De Bernardi, 2009; Ward & Tockner, 2001). 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 consolidation operations often accompany large river restoration projects. Provided that they integrate modern principles of ecological landscape planning, 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 habitat features, adjacent to the river outside the levees. These key habitat features are natural structures particularly important for biodiversity (ponds, stone piles, bushes, etc.), which are now absent from modern alluvial plain landscapes. Although this approach may be

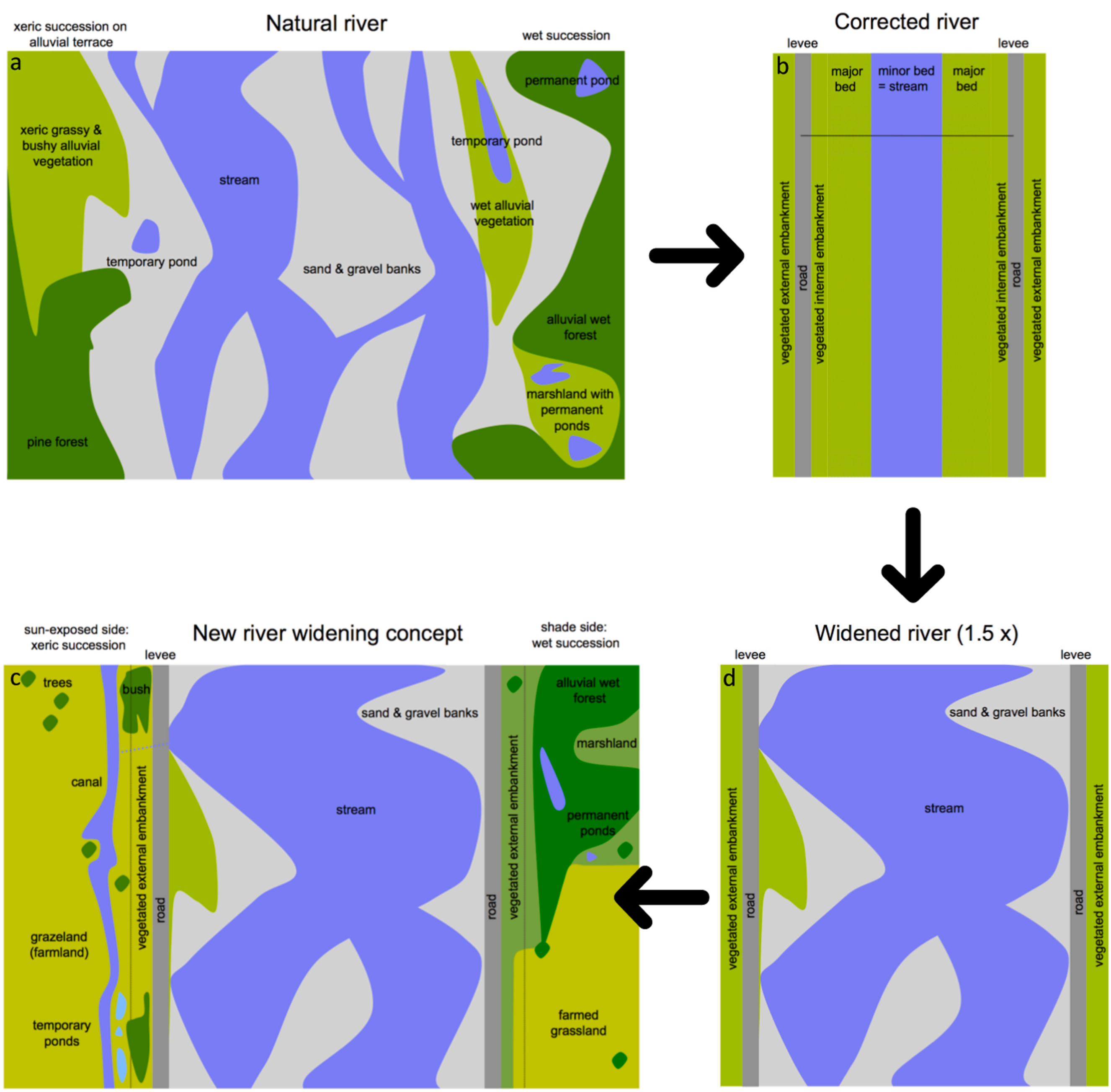

Fig. 1. Own schematic representation of (a) a natural river, (b) a conventionally corrected river, (c) a river widened by a factor 1.5 with additional buffer zones outside the levees, (d) a river restored with today's standard of widening the bed by a factor 1.5 without a buffer zone. C illustrates the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

limited for restoring lateral connectivity for aquatic organisms, as the surface hydrological connection to the main river channel is interrupted by the levees and only connections through the underground water can be maintained, it may considerably improve longitudinal connectivity for terrestrial and semi-aquatic species.

In this study, a theoretical re-allocation of agricultural habitats, as typically resulting from land consolidation 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 (Canton-of-Valais, 2015; Summermatter, 2004). 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 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 infrastructure and economic activities from future floods, but also to compensate the numerous ecological deficits that emerged after the former two drastic river bed corrections (Canton of Valais, 2015). Associating a biodiversity-rich, extensively-managed agricultural buffer zone (equipped with specific habitat features) outside the embankments all along the river, where feasible, would represent a major biodiversity asset, by substantially enhancing longitudinal and partially also lateral ecological connectivity.

To design such a network of semi-natural habitats, five key questions need to be addressed: (i) how can land consolidation measures (via farmland re-allocation) that generally accompany major river restoration operations be optimized for improving 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 habitat features fulfilling the requirements of these target species?; and (v) how should these habitat features be arranged in space from a multi-species perspective?

We simulated this planning process, using the Rhône river as a case example. First, we drew a digital map that enabled regrouping along the river, where possible, all grasslands (i.e. meadows and pastures) scattered throughout the plain so as to constitute the buffer habitat matrix. Second, we selected emblematic, endangered species, representative of complementary habitat needs, defined their ecological requirements (habitat patch size and connectivity for dispersal) and key habitat features. Third, we designed a spatial arrangement of these habitats that would enable their conjunct co-occurrence all along the buffer zone. In this context we addressed the specificity of riverside ecosystems which are longitudinal in essence, while connectivity indices and measures in metapopulation dynamics conceptual frameworks are mostly considering isotropic configurations (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, based on simulations, we tested whether there are major differences between an isotropic and longitudinal configuration of key habitats, which would imply different spatial constraints for planning valuable habitat features for biodiversity.

2. Material and methods

2.1. Study site

Our model region was a stretch of the Rhône River between the cities of Sierre and Martigny (Valais, SW Switzerland; 46°19′ N; 7°27′ E). We focused exclusively on the floodplain, from the river to the foothill contact line (according to the criteria of the Swiss Federal Office for Agriculture), corresponding to 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, in some parts immediately adjacent to the river.

2.2. 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 types in the 17 political communities of the study area, as provided by the cantonal authorities. As our analyses were restricted exclusively to grasslands on the plain, communities without agricultural land on the plain were excluded. The total area of overall grasslands and of biodiversity promoting area (hereafter BPA) grasslands was then calculated both per community and by pooling all the 16 retained communities together. With the help of the land cover maps and visual assessment using Google Maps, we assessed where along the foreseen (revitalized) riverbed a biodiversity-friendly grassland buffer zone could be realistically implemented, restricting the area to the farmland zone, i.e. excluding sealed areas and those stretches along the Rhône where the railway and highway were directly adjacent to the river. The lengths of the remaining stretches were measured. The width of a possible buffer zone along the Rhône was calculated assuming two scenarios. First, the sum of the grassland areas of each community was divided by the length of the river stretch owned by the respective community, in order to estimate the possible buffer width per community. In a second scenario, we redistributed the total available grassland area at valley bottom evenly among the communities so as to obtain a biodiversity buffer of equal width along the whole river stretch, independently of landownership.

2.3. Target species

We focused on a set of target species with complementary ecological requirements, so as to represent different habitat elements, area needs and dispersal abilities. The target species were 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. We considered three main habitat types, naturally occurring along riverine ecosystems in the study region: (1) xeric (grassland) habitats with natural structures; (2) tall trees and fruit trees among extensively-managed grasslands; (3) ponds. Two target animal species were selected for each type (Table 2). Only species enlisted in the Swiss list of national priority species (FOEN, 2010) were taken into account. Species-specific habitat requirements and dispersal abilities were assessed based on a literature search using Web of Science and Google Scholar, with precedence given to peer-reviewed literature, i.e. evidence- over expert-based references.

2.4. Effect of spatial habitat arrangement on metapopulation persistence

Longitudinally arranged habitat patches may not provide equally good conditions for metapopulation persistence as the same amount of habitat arranged in an isotropic network, due to a lower number of neighbouring patches within dispersal distance. To compare population persistence in longitudinal and isotropic habitat configurations, Hanski's metapopulation model (Hanski & Ovaskainen, 2000; Hanski, 1994, 1999) was applied:

$$S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij}) A_j \tag{1}$$

where S_i is the population dynamic connectivity of a patch i, $1/\alpha$ being the average dispersal distance, d_{ij} the distance of patch i to patch j and A_j the area of patch j. The model can be expressed by a matrix M consisting of

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

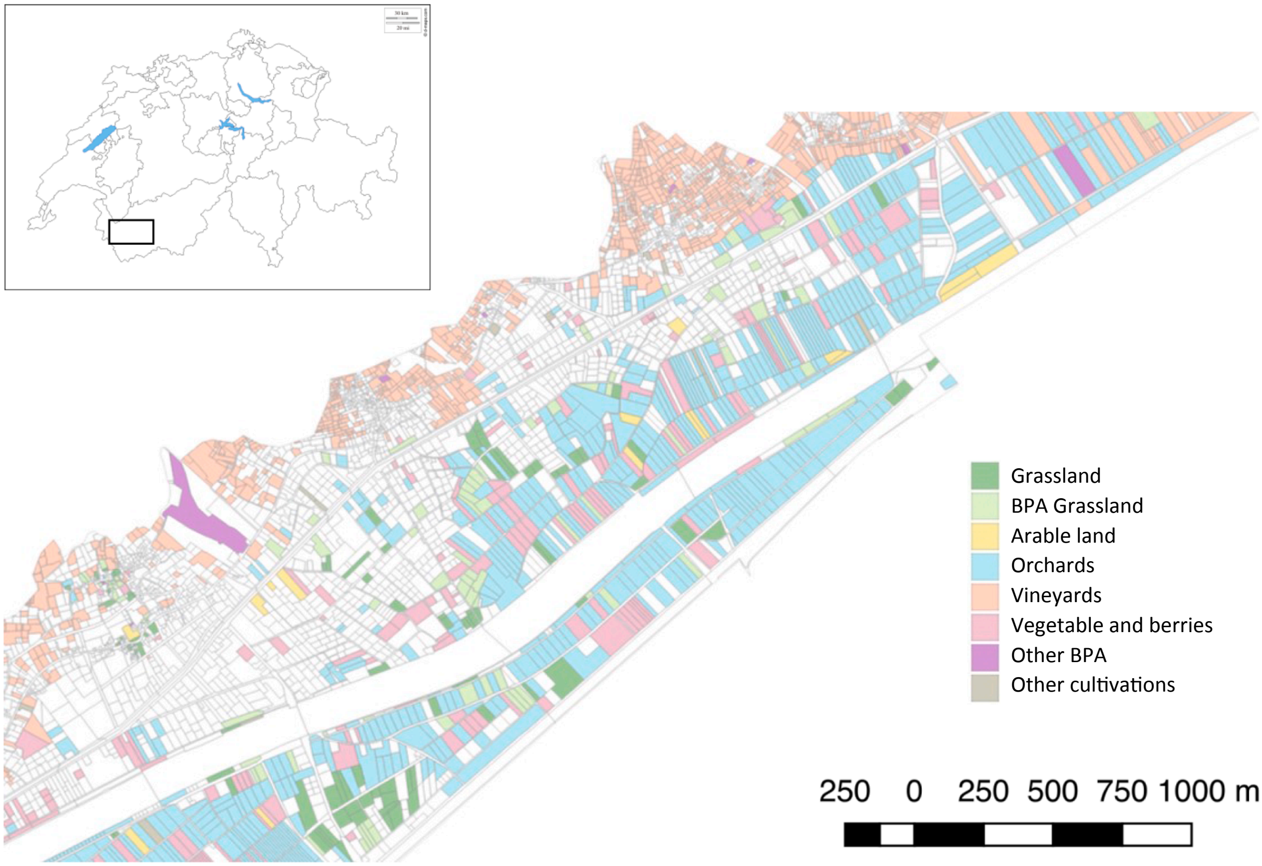

Fig. 2. A section of the alluvial plain in our study area (Fully, Valais, SW Switzerland) showing the scatter of the different agricultural types, notably that of grasslands. Regrouping these grasslands along the Rhône in a buffer zone would not only promote biodiversity but also contribute to rationalise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

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 $\lambda_M > E/C$ 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 (Appendix A), which yields as output whether a species is able to persist in the landscape. To compare species persistence under different options of habitat configuration (longitudinal vs isotropic), distance matrices were derived from patches arranged in a hexagonal grid (isotropic configuration) or a line (longitudinal configuration) both assuming equal next-neighbour distances and a similar number of habitat patches. 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 both configuration types, incrementally increasing habitat patch sizes (10–1000 m^2) and next-neighbour distances (100–5000 m) with different average dispersal

Table 1
Grassland area (biodiversity promoting area (BPA) 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
Mean	148′734	589′368	2′948	75	282

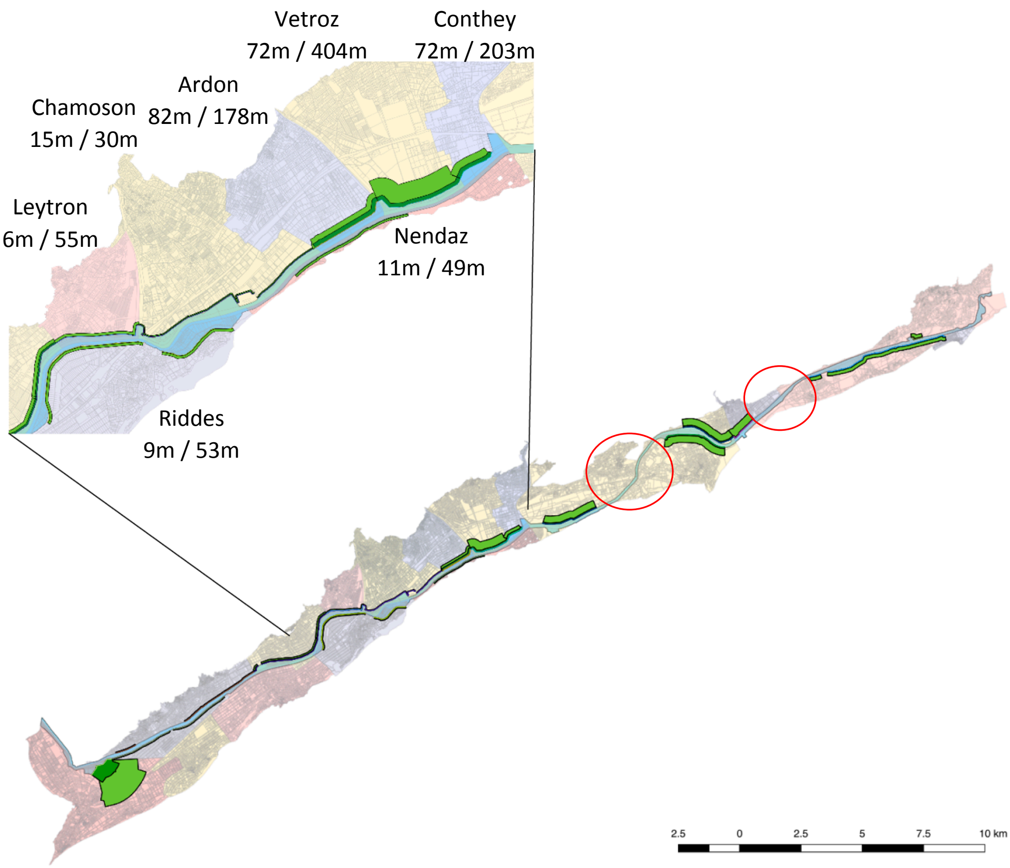

Fig. 3. Potential buffer zones (BPA grassland (dark green), or all grasslands together (light green), respectively) resulting from a redistribution along the Rhône of the grasslands available per community. A community-level approach delivers very heterogeneous widths of buffer zones and strips along 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 infrastructure are indicated by the two red circles. Different colours (yellow, red, blue) indicate different communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

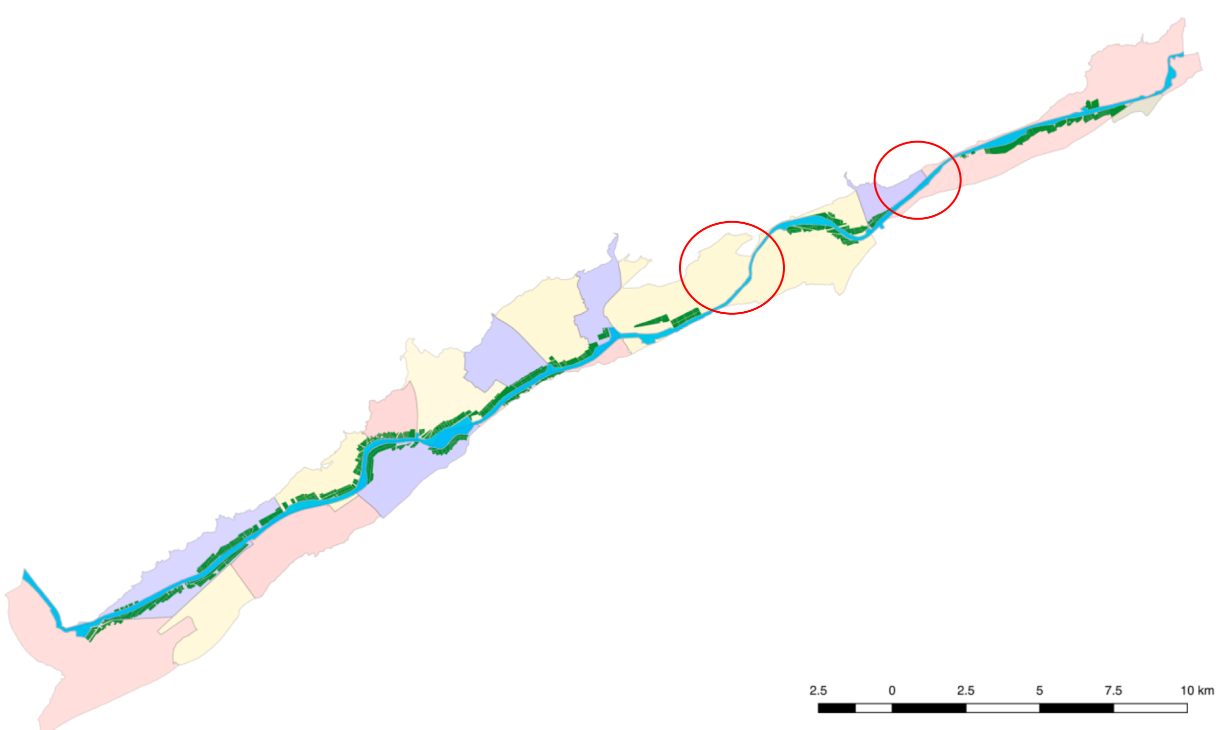

Fig. 4. Potential buffer zone (200 m broad, dark green) resulting from a redistribution of all the grasslands available across the study area along the Rhône. A regional approach delivers a homogeneous buffer zone that would contribute to restore both lateral and longitudinal ecological connectivity. Note the two major residual connectivity gaps (>2 km), due to human settlements and infrastructure, that cannot be eliminated (red circles). Different colours (yellow, red, blue) indicate different communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

capacities (50, 100, 150, 200, 250, 300, 500 m). In addition, referring to our model region, different land-improvement scenarios were simulated, with different widths of the buffer zone (50 and 200 m, respectively) and differences in the available grassland area, i.e. inclucing BPA grasslands only or considering all grasslands pooled together, respectively. All analyses were done in R studio with R 3.2.4 (R-Core-Team, 2016).

3. Results

3.1. GIS-modelling of the buffer zone

There were six different types of agricultural land use in the study area in decreasing order: fruit tree plantations (33% of the farmed area), vineyards (26%), conventional grasslands (18%), biodiversity promoting areas (BPA – extensively managed) grasslands (7%), arable land (6%), vegetable & berry cultures (5%), other types of BPA (2%) and other cultures (3%) (Fig. 2). Only conventional and BPA grasslands were retained for calculating the area theoretically available for constituting the buffer zone, resulting in 943 ha of general grasslands, including 237 ha of BPA grassland. The total length of the theoretical biodiversity-friendly grassland buffer (after removing sealed areas and infrastructure) would amount to 21.7 and 25.3 km along the southern and northern Rhône banks, respectively, stretching along 46.5% of the river line. Because grassland availability varied considerably between administrative units (Table 1) (16 communities with a total of 999 BPA grassland fields and 2′805 other grassland fields), 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). Three communities provided no room for a biodiversity buffer: the riverside of Chippis area was totally impervious, Charrat territory did not touch the river, while Saxon harboured a highway all along its stretch of the Rhône. Reshuffling the available grasslands across communities yielded an average buffer zone of 50 m or 200 m, respectively, depending on whether only BPA grasslands or all grasslands were considered (Fig. 4). There were two major unavoidable spatial gaps, however: the eastern gap is due to the highway running directly adjacent to the Rhône and the presence of a golf course, while the western gap is created by the city of Sion, the chieftown of Valais.

3.2. Target species

We selected six target species, two birds, a reptile, two amphibians and a lepidopteran species, representing different habitat feature types which can be created within the matrix of the buffer zone (Table 2). Thereby the levee embankments and the plain offer different microtopographical situations that can be taken advantage of: 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 (Fig. 5). 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.

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 birds, dispersal capacity plays no role within our regional system. This provided the basis for defining patterns of spatial recurrence of these habitat features that would guarantee the persistence of functionally connected metapopulations.

3.3. Effect of spatial habitat arrangement on metapopulation persistence

Under equal conditions regarding patch sizes and next-neighbour distances, metapopulation persistence was slightly higher in isotropic compared to longitudinal habitat systems. These differences were consistent across all scenarios (Fig. 6, Appendix B), yet they remained small at the tested scales, mostly below 10%. Let's illustrate this with an example: A hypothetical model species A with an average dispersal distance of 150 m would persist in an isotropic habitat configuration with a habitat patch size of 400 m^2 when patches are approximately 2′250 m distant. In contrast, the probability of species persistence in a longitudinal habitat system with the same inter-patch distance would be 10% less (Fig. 6b). Generally, the higher the average dispersal rates, the smaller the differences between the two models were. Our simulations suggest that for species with a dispersal distance of more than 500 m the colonisation potential of a suitable habitat patch of 150 m^2 or more is guaranteed in all cases.

4. Discussion

This study illustrates how the land consolidation operations that typically accompany major river restoration programmes can be used

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

Habitat type	Species	Habitat feature (structural element)	Area of territory	Maximum dispersal distance	Source
Xeric habitats with microhabitat structures	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, Böhme, Schneeweiß, Fritz, Schlegel, & Berendonk, 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 et al., 2007; Sierro, 2007; Heer, Pellet, Sierro, & Arlettaz, 2013
Trees and woody elements	Scops owl (*Otus scops*)	Tall trees with cavities or nest boxes every 350 m	10 ha grassland per pair, rich in bush crickets	beyond the maximal distance of the study area	Glutz von Blotzheim & 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	beyond the maximal distance of the study area	Glutz von Blotzheim & Bauer, 1993
Aquatic elements /ponds	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, & Schmidt, 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 et al., 2013

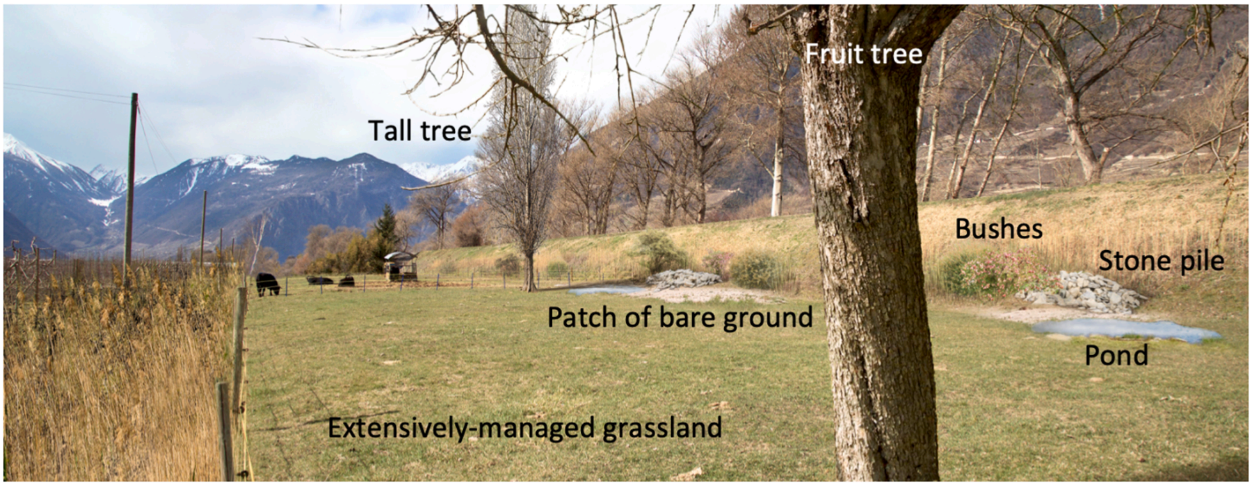

Fig. 5. Photomontage of the potential buffer zone along the Rhône river (levee visible on the right) as envisioned in this study, with the required habitat features for the six target species: pond for *Bufo bufo* and *Bombina variegata*; stone piles associated with bushes (notably *Colutea arborescens*) and patches of bare ground for *Lacerta bilineata* and *Iolana iolas*; tall trees and fruit trees among extensively-managed grasslands for *Otus scops* and *Lanius senator*.

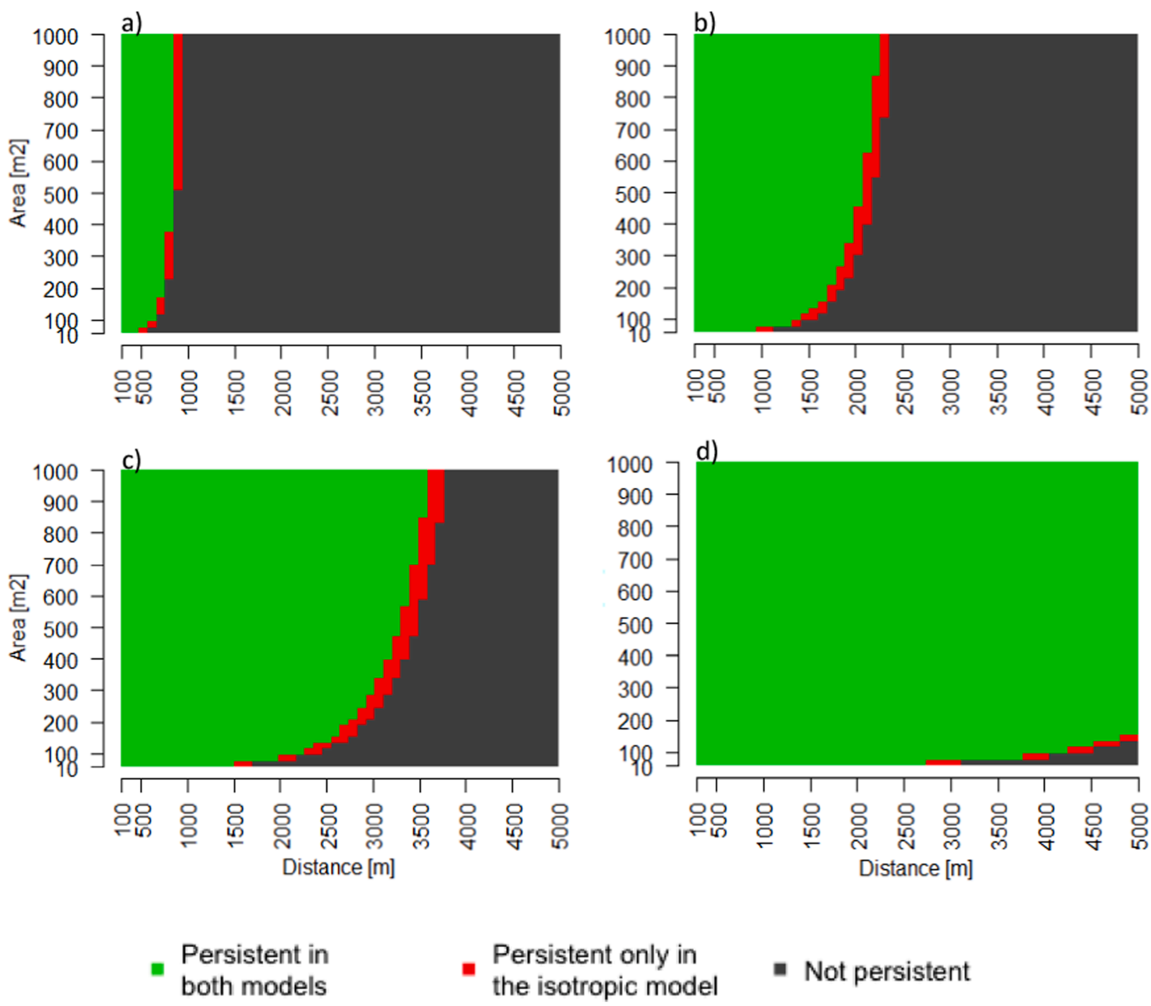

Fig. 6. Differences between *meta*-population persistence under an isotropic vs longitudinal configuration of the grassy buffer zone. We focused on the sole BPA grasslands (237 ha in total) for conducting these simulations, using a constant buffer width of 50 m. Simulations were calculated for species with different dispersal distances: a) 50 m, b) 150 m, c) 250 m and d) 500 m. Metapopulation persistence is only slightly affected by habitat configuration, whereas dispersal capacity is key, which calls for a regular spatial recurrence of habitat features along the buffer strip, with inter-patch distances corresponding to the dispersal capacity of the target species.

for re-allocating the farmland habitat with the highest value for biodiversity (e.g. extensively-managed grasslands) along rivers in order to improve the longitudinal and partially lateral ecological connectivity that nowadays crudely lacks in corrected streams. By associating to a grassland matrix natural and semi-natural key habitat features that can promote locally rare, emblematic species, general conditions for biodiversity could be greatly enhanced. Our analysis also suggests that environmentally friendly land consolidation measures would benefit from being integrated into a regional master plan, i.e. be planned beyond local community boundaries across a region, so as to obtain a homogeneous and continuous 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 as many species such as amphibians have terrestrial life stages (e.g. Rudolph & Dickson, 1990; Semlitsch & Bodie, 2003; Marty, Angélibert, Giani, & Joly, 2005). In the study area, such an herbaceous, 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 poor current ecological situation and may contribute to improving lateral connectivity. Although the levees will still constrain lateral connectivity to some extent at ground level, this approach would contribute to developing the Rhône River towards a functional ecosystem (Ward, Tockner, & Schiemer, 1999). Secondly, creating a regular spatial recurrence of the foreseen habitat features within the grassy buffer zone is also likely to enhance the regional conservation status for our array of target species, since they have mostly vanished following habitat degradation and destruction by agricultural rationalisation (Benton, Vickery, & Wilson, 2003; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Vickery & Arlettaz, 2012). It is important to recognize, however, that only a combination of the targeted species-specific habitat features with a non-hostile (here grassy) matrix is able to improve conditions for biodiversity in such a system. In effect, the grassy matrix operates as a green corridor facilitating dispersal movements, whereas the natural structures (piles of dead wood and stones, bushes, etc.) contribute to creating 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, i.e. without fertilization and via low-intensity grazing or mowing as it is the case in BPA grasslands, the grassy buffer matrix will not only increase landscape permeability for terrestrial biodiversity but also improve foraging conditions overall (Janin et al., 2009; Ray, Lehmann, & Joly, 2002; Salazar, Montgomery, Thresher, Macdonald, & Lötters, 2016). Finally, the spatial recurrence pattern of the dedicated habitat features will be key to reinstate 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 through spontaneous recolonization.

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 have been set to 1. The limit of our approach is therefore that it is mostly theoretical. This notwithstanding, the simulations show that a species facing an isotropic habitat configuration has a higher probability of persistence in the landscape than if subjected to an elongated environment, which is well supported by empiric data (e.g. Petren & Case, 1998; Kerr, Southwood, & Cihlar, 2001; Rahbek & Graves, 2001; Johnson, Frost, Mosley, Roberts, & Hawkins, 2003). However, this slight difference remains negligible from a landscape restoration designing viewpoint at the considered scale. More important, in contrast, is the spatial interval of recurrence of the habitat features within the grassy buffer matrix, which must be defined based on species' dispersal ability. The trade-offs between habitat patch size and inter-patch distance observed in our simulations indicate that species with sufficient dispersal abilities 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 our terrestrially-dispersing target species, and by extension any species that could be associated with them and profit from the same habitat features, 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.

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 (i.e where there is neither settlements nor heavy infrastructure). This is precisely what is proposed in this study, by regrouping along the river the numerous grassland patches scattered on the plain in order to constitute a continuous and functional ecological buffer. Both calculated scenarios (integrating all grasslands or only BPA grasslands, respectively) would offer excellent conditions for restoring longitudinal connectivity along the considered Rhône stretch. This buffer would still remain 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), alleviating the agricultural contstraints arising from small grassland fields scattered all over the floodplain. Due to the constraints given by landownerships and farming requirements, we focused only on the re-allocation and amelioration of grassland patches. However, converting part of this buffer zone into riverine forest habitats may represent an additional asset in restoring river ecosystem functionality (Gurnell, England, & Burgess-Gamble, 2019).

Clearly, however, only a collective approach involving all regional farmers and stakeholders would guarantee successful implementation (Arlettaz et al., 2010; Knaus, Laule, Kröpfle, & Landolt, 2016; Naiman, Decamps, & Pollock, 1993). 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 re-allocated). In case of massive resistance or will to maintain grasslands elsewhere on the plain, a solution would be to re-allocate 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, a spatial aggregation of the most valuable grassland habitats next to the revitalised river would benefit biodiversity by enhancing metapopulation functionalities with regard to both lateral (grassy-riparian-riverine habitat) and longitudinal connectivity. 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 et al., 1993). In the context of the Rhône river, two unavoidable gaps in longitudinal connectivity were identified, due mainly to urbanisation (Figs. 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 provided that some targeted habitat measures are implemented (Tanner & Gange, 2005), but the western gap 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, Chen, Tu, & Fu, 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.

One major conclusion of this study is that land consolidation 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.

5. Authors' contributions

Veronika Braunisch, Jérôme Pellet and Raphaël Arlettaz contributed with their ideas to the design. Jasmin Knutti modelled the buffer zones, did the literature research and ran the simulations. Jasmin Knutti and Raphaël Arlettaz led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2021.126062.

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