



Changing climate requires shift from refugia to sanctuaries for floodplain forests

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Received: 1 September 2020 / Accepted: 20 February 2021 / Published online: 19 March 2021
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Abstract

Context Riparian areas are considered to undergo major alterations under changing climate, making floodplain habitats targets for conservation and landscape planning. Protected areas might provide sanctuaries especially for sessile riparian plant species, but these niches are not always persistent over time.

Objectives We investigate if plant species of floodplain forests are provided with suitable habitat within currently protected areas and if these refugia persist. A coupled-modelling approach is used to gain spatially explicit information on new areas for sanctuaries.

Methods We use species distribution models to predict the niche of 12 *Salicion albae* and 7 *Fraxinion* floodplain forest species along rivers in Switzerland, under current, moderate and extreme climate change scenarios up to 80 years to the future (2100). The spread of plant species from current habitat to suitable future habitat is simulated using dispersal vectors and life history traits.

Results *Salicion albae* species are more flexible under both climate change scenarios than *Fraxinion* species. The main limitation for the spread of species is their dispersal ability, as only a minority of the suitable cells is colonized during the simulation process. The predicted future presence within currently protected areas decreases under both climate change scenarios in the model.

Conclusions Current protected floodplains do not provide persistent refugia for the plants studied, but might still be of importance to other organisms. Planning of sanctuaries for riparian plant species and communities need to focus on connectivity along rivers to maintain viable source populations in dynamic riverine landscapes under changing climate.

Keywords Riparia · Colonization · Floodplain forests · Dispersal · Species distribution model (SDM) · Climate change

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-021-01224-8>.

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Introduction

Over the last decade, the loss of wetlands including riverine floodplains was more rapid than any other ecosystem (United Nations 2018), although these ecosystems provide important services (Costanza et al. 1997), show higher species diversity than surrounding uplands (Brown and Peet 2003) and

harbor distinct plant communities (Sabo et al. 2005). Natural floodplain areas as well as typical floodplain vegetation depending on river dynamics are decreasing due to human impact e.g. by fragmentation due to dams (Jansson et al. 2000; Alldredge and Moore 2014; Pracheil et al. 2015) and altered river flow regime (Rivaes et al. 2015). Vulnerable riparian areas are a main target for conservation management and planning (Pullin et al. 2009), but few guidelines for riparian vegetation in a changing world exist (but see Dufour et al. 2019; Lind et al. 2019).

Riparian habitats along rivers are suspected to undergo major changes under climate change scenarios (Seavy et al. 2009; Mosner et al. 2015), since both climatic and hydrological factors will change and e.g. extreme floods might disrupt suitable habitat more frequently (Death et al. 2015). The local persistence of dynamic habitats is therefore expected to be reduced (Vittoz et al. 2013), which is especially disastrous for habitats which need several decades to establish, like floodplain forests of the plant community *Fraxinion* (Ellenberg 2010; Werth et al. 2012; Delarze and Gonseth 2015). These species rich plant communities (Ellenberg 2010; Delarze and Gonseth 2015) are crucial for the survival and spread of other organisms (Schnitzler-Lenoble and Carbiener 2007; Machar et al. 2019). Changing future climatic conditions also directly affect habitats close to the waterline, like floodplain forests of the plant community *Salicion albae*, which might result in modified plant communities due to e.g. longer drought periods followed by extreme floods (Ikeda et al. 2014; Chen et al. 2018).

Changing climate and its effect on riparian ecosystems has been investigated previously, indicating either threat of species loss or retreat to higher altitudes (e.g. see Garssen et al. 2014; Mosner et al. 2015). Conservation planning for vulnerable species and habitats within the diverse ecosystems is recommended to be done at the landscape context (Capon et al. 2013). Still, many processes responsible for riparian vegetation establishment and persistence along catchments remain unclear, although some models allow predictions by linking information on habitat formation and species abundance (Fink et al. 2017; Gostner et al. 2017; Caponi et al. 2019). Similarly, genetic analyses of riparian plants allow indirectly inferring processes of the past and present leading to the current distribution of species and gene pools as well as connectivity patterns along rivers

(Pollux et al. 2009; Cushman et al. 2014; Werth and Scheidegger 2014).

For the survival of riparian plant species, connectivity is crucial for the recolonization of suitable habitat (Ward et al. 1999). Therefore, sessile riparian plant species along rivers show adaptations to various types of dispersal, e.g. animal-mediated dispersal (Müller 1955; Ellenberg 2010), water-mediated dispersal (hydrochory, Nilsson et al. 2010), and wind dispersal (Ellenberg 2010), maintaining connectivity over long and short distances (e.g. *Ulmus laevis*, Venturas et al. 2014). Wind-mediated upstream dispersal was shown to be important for gene flow in many species (Wubs et al. 2016), while mainly vegetative diaspores and only few seeds are dispersed by water (Boedeltje et al. 2003).

As dispersal plays a key role for riparian plant species (Catford and Jansson 2014), including information on species' spread from currently occupied habitats to future potential areas allows to improve predictions for future species' occurrences (Engler et al. 2009). Landscape and conservation planning therefore uses modelling of current and future species' distribution to predict changes in functional connectivity among populations along a river (Inoue and Berg 2017) as well as to detect refugia, which are areas providing habitat for species during disturbance events and under changing climate (Morelli et al. 2016). While protected areas like parks and nature reserves might provide sanctuaries, which are temporarily suitable habitats for species e.g. under current climatic conditions, these might not be persistent over time and new protected areas might be necessary (D'Amen et al. 2011; Hannah et al. 2014a; Barrows et al. 2020; Morelli et al. 2020). Therefore, more riparian species have to be investigated to adjust conservation goals (Pullin et al. 2009; Driscoll et al. 2013).

This study aims at determining if plant species of floodplain forests find sanctuaries in protected areas and if these persist as refugia under both moderate and extreme climate change scenarios. If protected areas provide sanctuaries we hypothesize that suitable habitat is prevalent within the designated protected perimeter, and in the case of refugia, models should predict most of the future suitable habitat remaining inside the protected zone. We use species distribution models to investigate the niche and the current and future distribution pattern of 12 *Salicion albae* and 7 *Fraxinion* floodplain forest species along rivers in

Switzerland with citizen science and research data provided by the Swiss database for plants (Info Flora). To gain information for landscape and conservation planning of potential long term refugia and future sanctuaries as well as functional connectivity for floodplain forests, we simulate the spread of plant species using information on dispersal to potentially suitable future habitats along river catchments in Switzerland.

Methods

Study species

Typical plant species of the two plant communities of floodplain forest of the lowland (*Salicion albae*) and floodplain forest of a later successional stage (*Fraxinion*) were investigated in this study (see Table 1). *Salicion albae* habitats are listed as endangered in Switzerland (BAFU 2011; Delarze et al. 2013), while *Fraxinion* floodplain forests are described as a habitat type worth protecting by the Federal Act of Protection of Nature and Cultural Heritage (1966) as they have very long regeneration time of 50 to 200 years (Delarze et al. 2013; Delarze and Gonseth 2015). Species for the current study were selected based on the list of Swiss national priority species (BAFU 2011), representing indicator species for habitat types and therefore include redlisted and target species for conservation projects, and data availability at the Swiss National data base Info Flora (www.infoflora.ch, as of December 19, 2016). This data base collects occurrence data obtained in research and monitoring projects under the supervision of the Federal Office for the Environment of Switzerland, Swiss cantonal authorities, non-profit organizations as well as data collected by citizens. We obtained data for twelve *Salicion albae* species (two tree species, six shrub species, and four herbaceous species) and seven *Fraxinion* species (two tree species, four sedges, and one herbaceous species, see Table 1 and Table 2) along all waterways in Switzerland. Data selection for all analyses included the following precautions: only coordinates with a precision of ≤ 100 m and collection dates between 1960 and 2015 were used. All locations of species' occurrence were transformed to a raster of 100×100 m using the raster package in R (Hijmans and van Etten 2012)

covering whole Switzerland including all catchments. Duplicates were removed and only one presence point per grid cell was kept to avoid spatial autocorrelation in the niche modelling approach (Guisan and Zimmermann 2000). The data was used in a hierarchical framework by first modelling suitable habitat and subsequently simulating the spread of species from recorded sources to predicted suitable habitat, also taking into account changing climate.

Modelling habitat suitability

Data from nine uncorrelated geological, topographic and climate predictors (see Fink and Scheidegger 2018) were applied to define the current ecological niche of the species in Switzerland: Mean annual temperature, mean annual precipitation (sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, prepared by the division of Landscape Dynamics of WSL, following the methodology used in Thornton et al. 1997), wetness index (following Tarboton 1997, see in Camathias et al. 2013), nutrient-holding capacity, northness, slope, soil permeability, water-holding capacity and hydrometric properties (Camathias et al. 2013). To account for proximity of habitats to rivers in Switzerland, all predictor layers were masked to only cover 1000 m around rivers within Switzerland in arcGIS (ESRI 2015). Habitat suitability for the reference period (1960–2013) was modelled using the software Maxent (Phillips et al. 2006). The reference period is shorter than the species record period to ensure that a majority of species have reach maturity for subsequent dispersal simulation (see below). We sampled 10'000 background points and performed a ten-fold-crossvalidation (Phillips et al. 2009). Models were evaluated for predictive power by the area under the curve (AUC) of the receiver operating characteristics (see Phillips et al. 2006) and by Boyce index using the ecospat package in R, applying a sliding window (Hirzel et al. 2006). The same R package was used to calculate and visualize the correlation between the ratio of predicted to expected species presences (Hirzel et al. 2006).

Table 1 Dispersal kernels and other life history traits of *Salicion albae* and *Fraxinion* species

Name	Dispersal vector	Dispersal model	Dispersal vector in model	Long distance dispersal	Age of first reproduction	Propagule production vector	Reference
<i>Salicion albae</i> species							
<i>Epipactis rhodanensis</i>	Wind	Negative exponential	c(0.7857, 0.1753, 0.0390)	no	10	c(0.1, 0.5)	Adapted from (Bill 2000)
<i>Myosoton aquaticum</i>	Gravity	Uniform distribution	c(0.1)	no	1	c(0.1, 0.5)	(Müller and Scharm 2001)
<i>Populus</i> ssp. (<i>P. alba</i> , <i>P. nigra</i>)	Wind	Negative exponential	c(0.5392, 0.2975, 0.1633)	yes	10	c(0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9)	(Müller 1955; Ellenberg 2010; Debeljak et al. 2015)
<i>Salix</i> ssp. (<i>S. alba</i> , <i>S. fragilis</i> , <i>S. myrsinifolia</i> , <i>S. purpurea</i> , <i>S. triandra</i> , <i>S. viminalis</i>)	Wind	Negative exponential	c(0.9008, 0.0376, 0.0616)	yes	6	c(0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9)	(Chmelar and Meusel 1979; Gage and Cooper 2005; Ellenberg 2010)
<i>Solanum dulcamare</i>	Bird, snail	Uniform distribution	c(0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1)	yes	1	c(0.1, 0.5)	(Müller 1955; Ellenberg 2010)
<i>Symphytum officinale</i>	Gravity, occasionally ants	Uniform distribution	c(0.1)	no	1	c(0.1, 0.5)	(Müller 1955)
<i>Fraxinion</i> species							
<i>Carex</i> ssp. (<i>C. brizoides</i> , <i>C. pendula</i> , <i>C. remota</i> , <i>C. strigosa</i>)	Wind, water	Inverse Power	c(0.8679, 0.0812, 0.0509)	yes	2	c(0.1, 0.5)	(Müller 1955; Pijl 1982; Müller-Schneider 1986; Cappers 1993; Bill 2000; Gizaw et al. 2016; Marquez Corro et al. 2017)
<i>Malaxis monophyllos</i>	Wind, gnats	Uniform distribution	c(0.1)	yes	10	c(0.045)	(Rakosy 2014; Jermakowicz et al. 2015, 2017)
<i>Prunus padus</i>	Bird	Uniform distribution	c(0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1)	no	2	c(0.125, 0.25, 0.375, 0.5, 0.625, 0.75, 0.875)	Adapted after (Heller and Zavaleta 2009; Ellenberg 2010; Breitbach et al. 2012)
<i>Ulmus laevis</i>	Wind	Uniform distribution	c(0.1)	yes	10	c(0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9)	(Venturas et al. 2014)

Table 2 Overview of model precision and predicted suitable and unsuitable habitat for the calibration period (1960–2013)

	Presence points	AUC	Std AUC	Spearman corr	Cells	
					Predicted presence [%]*	Predicted absence [%]
<i>Salicion albae</i> species						
<i>Epipactis rhodanensis</i>	100	0.974	0.022	0.883	5.0	95.0
<i>Myosoton aquaticum</i>	301	0.887	0.025	0.993	15.4	84.6
<i>Populus alba</i>	279	0.919	0.032	0.998	11.9	88.1
<i>Populus nigra</i>	276	0.916	0.021	0.994	12.0	88.0
<i>Salix alba</i>	668	0.903	0.016	0.998	12.4	87.6
<i>Solanum dulcamara</i>	844	0.857	0.016	0.999	17.7	82.3
<i>Salix fragilis</i>	72	0.896	0.044	0.976	15.5	84.5
<i>Salix myrsinifolia</i>	475	0.826	0.036	0.989	20.5	79.5
<i>Symphytum officinale</i>	700	0.891	0.023	0.994	14.2	85.8
<i>Salix purpurea</i>	744	0.867	0.017	0.981	16.1	83.9
<i>Salix triandra</i>	113	0.907	0.041	0.956	13.4	86.6
<i>Salix viminalis</i>	165	0.892	0.022	0.992	14.0	86.0
<i>Fraxinion</i> species						
<i>Carex brizoides</i>	163	0.84	0.046	0.984	16.0	84.0
<i>Carex pendula</i>	364	0.835	0.023	0.998	21.4	78.6
<i>Carex remota</i>	515	0.827	0.026	0.999	22.1	77.9
<i>Carex strigosa</i>	150	0.943	0.022	0.985	9.5	90.5
<i>Malaxis monophyllos</i>	355	0.947	0.014	0.992	8.3	91.7
<i>Prunus padus</i>	303	0.911	0.028	0.981	13.1	86.9
<i>Ulmus laevis</i>	46	0.873	0.067	0.964	17.1	82.9

*Cells with predicted distribution of species for reference period (1960–2013) along rivers in Switzerland

Predicted species distribution and Floodplains of National Importance

The average value of ten independent modelling runs resulted in a habitat suitability map with continuous probabilities for each species, and was transformed in species presence-absence maps. The binary maps were calculated using the equal training sensitivity and specificity logistic threshold (Liu et al. 2013) calculated by the software Maxent (Phillips et al. 2006). Raster cells with predicted presences for *Salicion albae* species and for *Fraxinion* species independently were overlapped and core areas forming ideal niches for the respective plant communities were identified in the program R (R Core Team 2016). Moreover, the predicted core areas as well as single species predictions were overlapped with areas of current protected floodplains (Floodplains of National Importance, legislation origination from 1992; Hausammann

et al. 2005). Number of cells within Floodplains of National Importance were compared to cells outside these protected areas using Welch t-tests in R (Welch 1947; R Core Team 2016).

Niche modelling under climate change

Future habitat suitability was modelled by projecting the model with the current niche definition to eight future time periods covering 10 years each (first period 2014–2023 up to last period 2084–2093) using Maxent (Phillips et al. 2006). While geological and topographic predictors remained constant in all simulations, layers of temperature and precipitation were once left unchanged (baseline simulation), but also modified according to two climate scenarios based on information of the coordinating body of CORDEX (see <http://www.euro-cordex.net>, as agreed on CMIP5 (IPCC Fifth Assessment, 2009). The first of two

climate scenarios applied was the regional climatic model CLMcom-CCLM4-8-17, calculated and downscaled from the global climatic model CNRM-CERFACS-CNRM-CM5 using emission predictions of RCP 4.5. The second scenario was based on the regional climatic model CLMcom-CCLM4-8-17 calculated and downscaled from the global climatic model ICHEC-EC-EARTH by ICHEC using emission predictions of RCP 8.5. Both data sets were further downscaled to a 100×100 m grid over Switzerland applying the Delta change method and using measured data on temperature and precipitation as a reference (data sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, data prepared by the division of Landscape Dynamics at WSL). The first model represents a moderate climate change with moderately increasing temperature, and only moderately increasing precipitation in winter compared to the reference period (1961–1990). The second scenario represents a more extreme climate change, with very dry summers and extreme temperature increases in comparison to the reference period (see in Fink and Scheidegger 2018). The two scenarios allow assessing the climate change impact on habitat availability by contrasting moderate and extreme changes in terms of temperature and precipitation.

Simulated dispersal to future habitat

For the simulation of the spread of species from current present points to future modelled suitable habitat along all Swiss rivers, we performed a literature search on life history traits of species including information on dispersal vectors and distances (see Table 1). Information on initial maturity and age dependent seed production were implemented in the model to simulate the spread under realistic assumptions. Literature data on dispersal vectors and distances was fit to dispersal models and dispersal kernels respectively (Table 1). Dispersal was simulated using the package MigClim 1.5 in R (Engler et al. 2012): There the kernel represents the probability of the spread of source cells to adjacent cells. For species displaying long-range dispersal (e.g. by water, birds or wind), it was included in the simulation with a low probability (0.01) up to distances of 10 km (Fink and Scheidegger 2018).

We simulated the dispersal from current species' occurrences for 50 and 80 years to the future, based on

the probability to reach the surrounding cells (dispersal kernel) and the probability of suitable habitat (habitat suitability maps). Starting with the reference time period (1960–2013), habitat suitability maps were updated five and eight times respectively during the dispersal simulation for each climate change scenario. Each simulation was repeated 100 times for each species and scenario. The average of the results of these simulations were used to compare the area of occupied and colonized cells after 50 and 80 years of dispersal in general and to the current areas of Floodplains of National Importance (Hausammann et al. 2005). Colonized cells are raster cells that became inhabited by the species in the course of the simulation, while occupied cells remain populated from the initial state to the end of the simulation (see in Engler et al. 2012). Contrary to that, decolonized cells were once inhabited by the species but do not remain populated till the end of the simulation due to habitat becoming unsuitable. Comparisons of occupied and colonized as well as decolonized cells at the end of simulations between different climate change scenarios were calculated using Welch's t-Tests (Welch 1947) and repeated measure ANOVA in R (R Core Team 2016). To analyze differences between catchments, the results were grouped by the four main catchments (Inn, Rhine, Rhone, Ticino), and the number of suitable but not colonized cells were determined for each catchment area using information on each tributary in arcMap (ESRI 2015).

Results

Modelling habitat suitability for the reference period

Maximum entropy modelling using the software Maxent (Phillips et al. 2006) resulted in models with AUC values indicating good prediction accuracy ($AUC > 0.75$, see Table 2 and compare to Manel et al. 2001). Model evaluations using the ecospat package showed high correlations between predicted to expected presence points and habitat suitability (Spearman correlation, 0.883 – 0.999, see Table 2 and Appendix for graphical representations, Figs A1). Average habitat suitability maps for whole Switzerland revealed that all species have independent niches (Appendix, Figs A2). Still, most *Salicion albae*

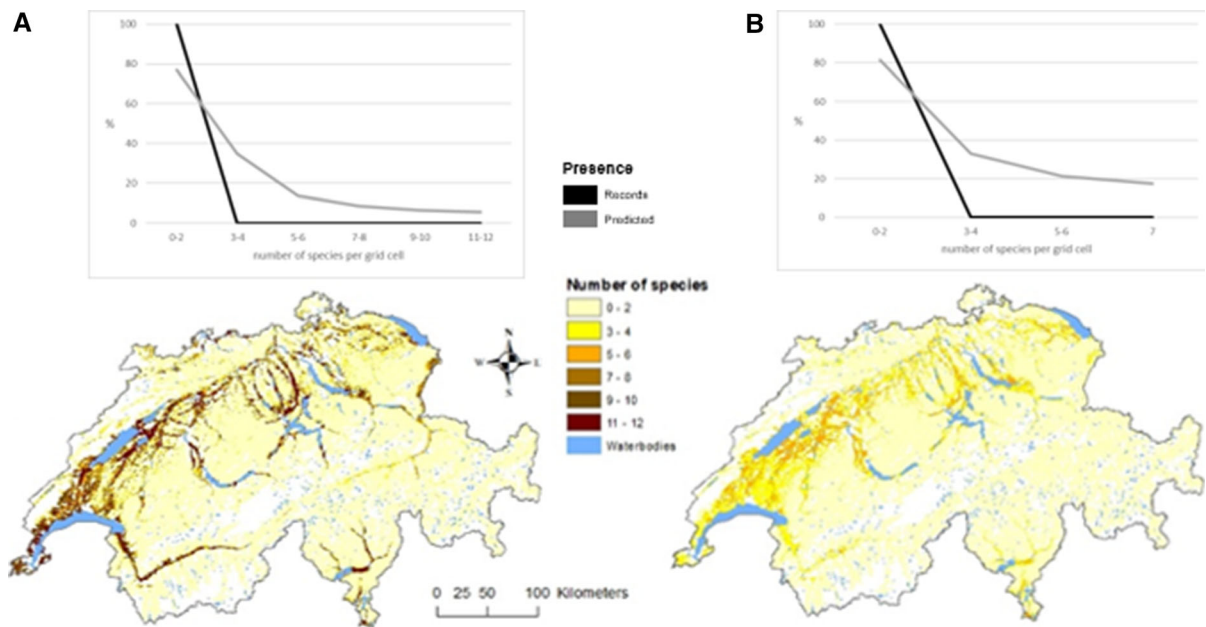


Fig. 1 Data records and modelled species distribution for characteristic plant species of *Salicion albae* (A, 12 species) and *Fraxinion* (B, 7 species) in Switzerland. Recorded and predicted species distributions per grid cell (above) show that more habitats are predicted to be suitable for the two plant

communities than recorded in the database. The map of predicted species distribution in Switzerland (below) shows that both plant communities are mainly predicted to occur along Rhine catchment (Central plateau), as well as Rhone and Ticino

species showed main suitable habitats along Rhine, Rhone and Ticino, except for *Epipactis rhodanensis*, for which suitable habitats are mainly found along Rhone and Rhine. For two species of this plant community (*Salix myrsinifolia* and *Salix purpurea*), models revealed suitable habitats along all four catchments equally (Inn, Rhine, Rhone, Ticino, see Appendix). Similarly, *Fraxinion* species showed many areas with high suitability along Rhine, Rhone and Ticino, except for *Carex strigosa* and *Malaxis monophyllos*, for which areas were limited to the Rhine catchments (see Appendix, Figs A2).

Predicted species distribution under current climate scenarios

Predicted distribution maps were obtained based on modelled habitat suitability maps (Fig A3). Major catchments with predicted species distribution are Rhine, Rhone and Ticino. One species of the *Salicion albae* community, *S. myrsinifolia*, has a widespread predicted distribution along all four catchments (see Fig A3). Similarly, for two *Fraxinion* species, *Carex pendula* and *Carex remota*, over 20% of cells were

predicted to be suitable (Table 2), while all other floodplain forest species display occupation of less than one fifth of all cells along rivers. Especially *C. strigosa* and *M. monophyllos*, two species of the *Fraxinion* community, reveal limited distribution mainly along Rhine catchment, and consequently low percentage of predicted distribution (9.5% and 8.3%, see Table 2 and Fig A3).

Pooled information on all 19 forest species revealed 46.1% of all cells without any predicted species and no cell with predicted presence for all species (Fig. 1). When only considering species of the *Fraxinion* community separately, no cells were detected where all 7 species were predicted, and only 1% of the cells were occupied by 6 out of 7 species. Additionally, 55.6% of all cells in Switzerland were predicted to be uninhabited by *Fraxinion* species. For species of the *Salicion albae* community, 1.1% of all cells of Switzerland were predicted to be occupied by all 12 species together, while 62.6% cells were predicted to be uninhabited.

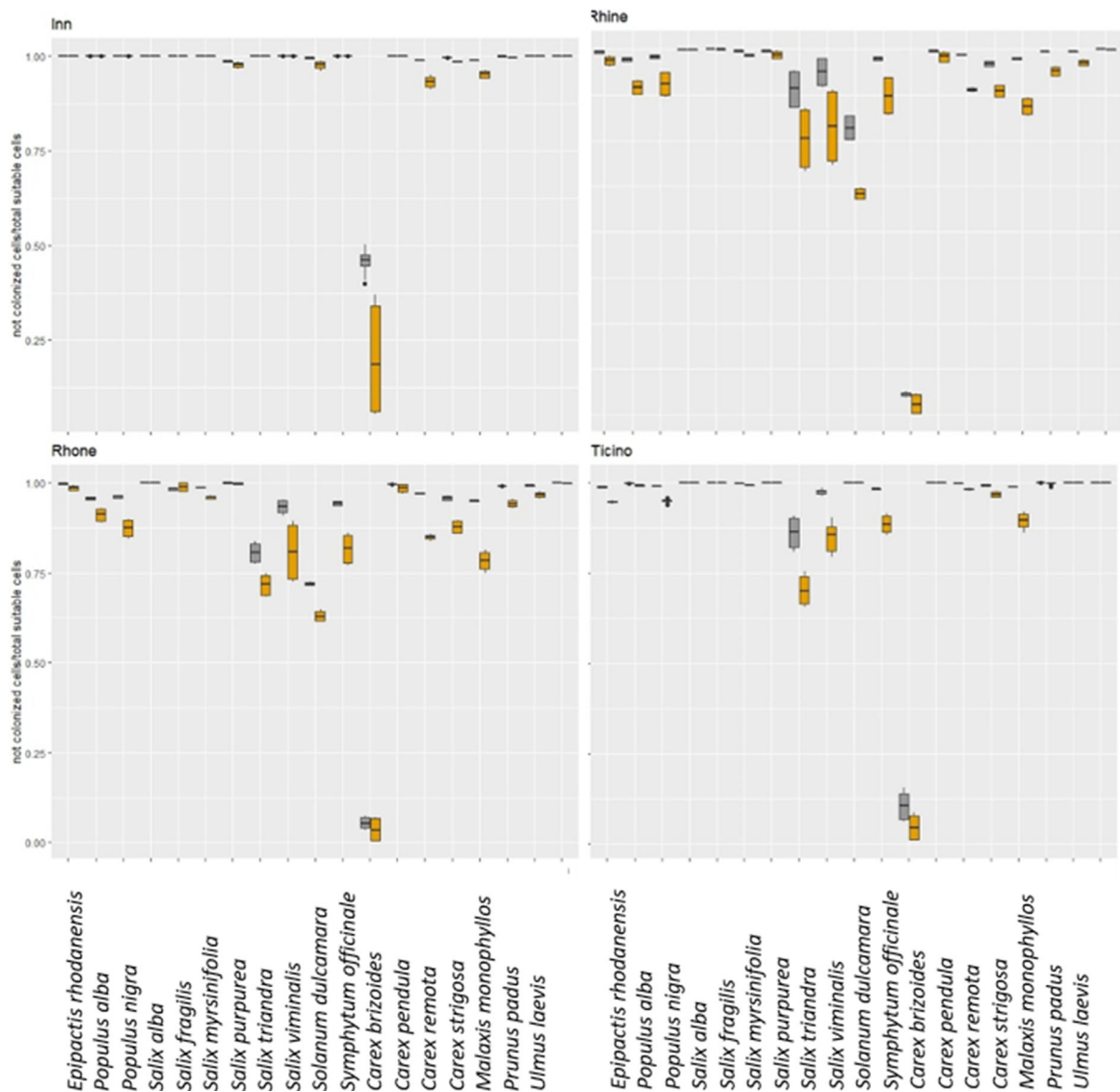


Fig. 2 Representation of cells which are potentially suitable but cannot be reached due to dispersal limitations along the four major catchments within Switzerland (Inn, Rhine, Rhone, Ticino). The difference between 50 (grey) and 80 years (yellow) of dispersal simulation under the assumptions of two climate

change scenarios reveals a complex pattern of uncolonized cells, indicating that not only dispersal limitations are responsible for the limited spread of species, but also changing habitat suitability (see text)

Niche modelling and simulated dispersal under climate change

Moderate and extreme climate change scenarios revealed generally similar prediction patterns of habitat suitability for both floodplain forest plant communities (see Supplementary material, Figure A2). While for a majority of the species of *Salixion albae*

the area represented as suitable habitat increased under both scenarios after 80 years from now, for all *Salix* species (except *Salix triandra*) the habitat suitability decreased (see Supplementary material, Figure A2). Similarly, for all *Fraxinion* species (except for *C. pendula*), habitat suitability decreased in predictions under both climate change scenarios.

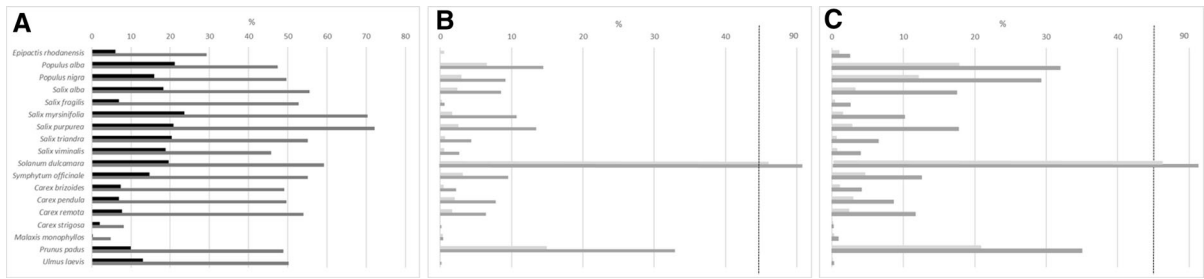


Fig. 3 Comparison of the percentage of the total area covered within the current protected Floodplains of National Importance of the actual reported presence of species (A, black), predicted occurrence for the reference period (A, grey), predicted colonized cells after 50 years (light grey) and 80 years (dark grey) of dispersal under moderate climate change scenarios

(B) and predicted colonized cells after 50 years (light grey) and 80 years (dark grey) of dispersal simulated under extreme climate change assumptions (C). The number of predicted colonized cells decreased under both climate change scenarios for most species except for *Solanum dulcamara* and *Prunus padus*

Simulations for the spread of floodplain forest species under dispersal assumptions revealed that although dispersal took place, significantly less cells were colonized (compared to uncolonized cells) for both plant communities under both climate scenario assumptions (*Fraxinion* species $t = -126.60$, $p < 0.01$; *Salicion albae* species $t = -92.27$, $p < 0.01$). Comparisons between the two climate change scenarios for each plant community showed significant differences in cells that remained occupied throughout the whole simulation both after 50 years ($t = -10.65$, $p < 0.01$) and after 80 years ($t = -10.85$, $p < 0.01$) for *Fraxinion* species. No difference in occupied cells was detected for simulations after 50 years ($t = -0.92$, $p = 0.98$) for *Salicion albae* species, but differences between occupied cells for simulations of different climate change scenarios were significant after 80 years of dispersal ($t = -20.06$, $p < 0.01$). For colonized cells, both plant communities showed significant differences after 50 (*Fraxinion* species: $t = -15.97$, $p < 0.01$; *Salicion albae* species: $t = -23.46$, $p < 0.01$) and 80 years (*Fraxinion* species: $t = -24.14$, $p < 0.01$; *Salicion albae* species: $t = -31.03$, $p < 0.01$).

Repeated measure ANOVA analysis for each species showed that the climate change scenario and the years of dispersal simulation both had a significant effect on the colonized cells during the simulation (repeated measure ANOVA, years: $F = 24.54$, $p < 0.001$; climate change scenario: $F = 12.45$, $p = 0.002$). Each catchment shows differences in predicted cells which could not be reached (suitable, but not colonized cells, see Fig. 2). Still, not only dispersal limitations were responsible for limiting the

spread of species, as the additional 30 years of dispersal (80 years compared to 50 years) do not result in less uncolonized cells for all species, for each catchment and also within the protected floodplain area (Figs. 2 and 3).

Predicted distribution Floodplains of National Importance and shifting sanctuaries

We checked for recorded and predicted species presence within currently protected Floodplains of National Importance, which make up 0.48% of the size of Switzerland (Fig. 3). For most of the floodplain forest species, approximately half the cells within floodplains were suitable habitat for the species under current climatic conditions, except for *S. myrsinifolia* and *S. purpurea*, where $> 70\%$ of the cells were suitable (Fig. 3, A). Contrary to that, *C. strigosa* and *M. monophyllus*, two species of the *Fraxinion* community, had $< 10\%$ of suitable cells within protected floodplain areas (Fig. 3, A).

The predictions for the cells being colonized within Floodplains of National importance under two climate change scenarios are much lower both after 50 and 80 years of dispersal (Fig. 3). The only exception is *Solanum dulcamara*, a species of the *Salicion albae* community, which shows a high number of colonized cells within the area of the current protected floodplains (Fig. 3), and which was also able to colonize all catchments (see Fig. 4).

The spatially explicit outputs of the simulations show which species is expected to colonize which areas along each catchment under each climate change scenario (for the extreme climate change scenario

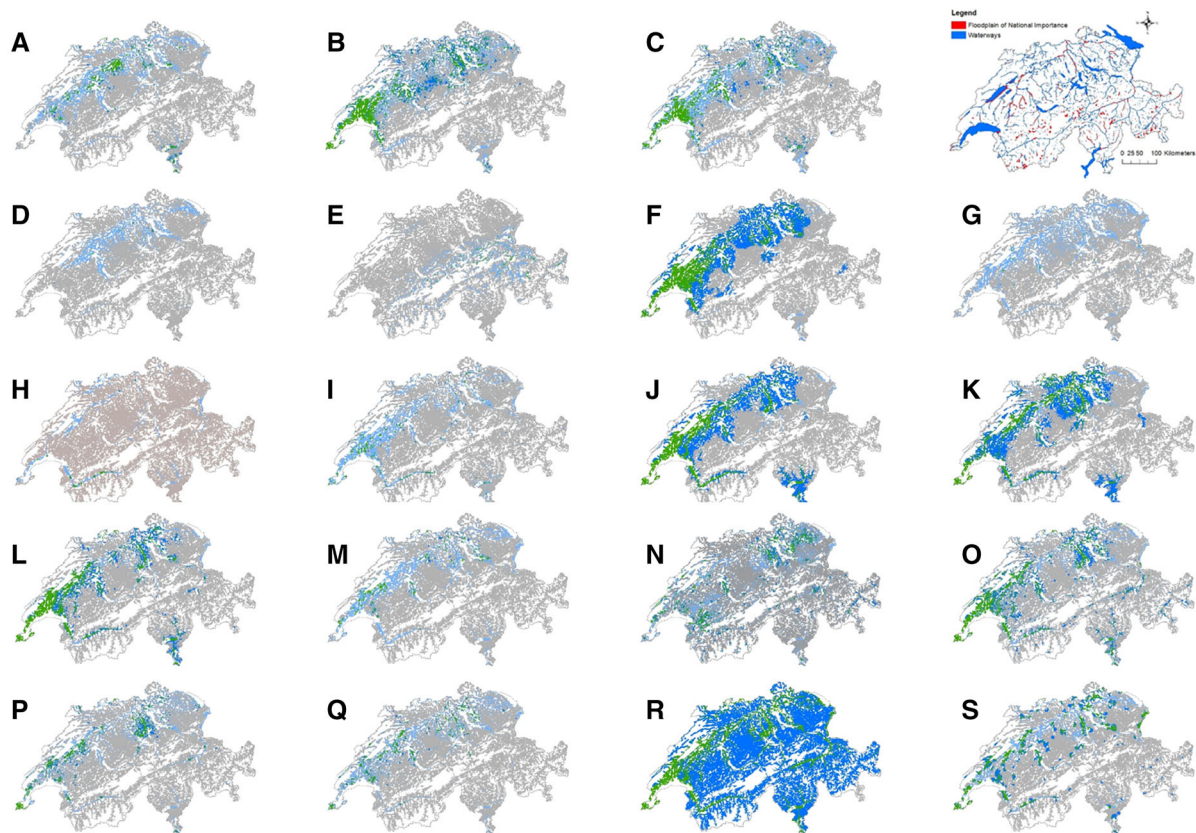


Fig. 4 Change in predicted distribution modelled under current climatic conditions which does not persist (light blue) and simulated colonized cells after 80 years of dispersal under the extreme climate change scenario which would not be occupied under current conditions (dark blue). Colonized or occupied cells under both current and future conditions are shown in green, while unoccupied (either unsuitable or uncolonized) cells throughout the simulation are shown in grey. Many species show large areas mainly along the Central Plateau which are not persistent refugia (light blue, e.g. *C. strigosa*, *U. laevis*,

S. fragilis), but few species can cope with changing climatic conditions and new sanctuaries appear (dark blue, e.g. *P. padus*, *P. alba*, *P. nigra*). Fraxinoin species: A) *Carex brizoides*, B) *Carex pendula*, C) *Carex remota*, D) *Carex strigosa*, E) *Malaxis monophyllos*, F) *Prunus padus*, G) *Ulmus laevis*; *Salicion albae* species: H) *Epipactis rhodanensis*, I) *Myosoton aquaticum*, J) *Populus alba*, K) *Populus nigra*, L) *Salix alba*, M) *Salix fragilis*, N) *Salix myrsinifolia*, O) *Salix purpurea*, P) *Salix triandra*, Q) *Salix viminalis*, R) *Solanum dulcamara* and S) *Symphytum officinale*

compared to the current climate change scenario, see Fig. 4). The *Salicion albae* species *S. dulcamara* is the only species which is able to colonize a majority of cells along all catchments even under the extreme climate change scenario (Fig. 4). Some species mainly colonize the Central plateau area, along the Rhine catchment (*C. pendula*, *C. remota*, *Prunus padus* and *Symphytum officinale*, see Fig. 4), while the two *Populus* species, *P. alba* and *P. nigra*, as well as *Salix alba* and *S. purpurea* colonized both the Rhine and the Ticino catchment under extreme climate change scenarios (Fig. 4).

Few species show areas of predicted distribution which persist under current and future climate scenarios (Fig. 4, e.g. *C. pendula*, *C. remota*, *P. padus*, *P. alba*, *S. alba*, *S. purpurea*, *S. dulcamara*). Contrary to that, it is predicted for many species that the area along the Central Plateau is not persistent habitat (Fig. 4, e.g. *C. strigosa*, *Ulmus laevis*, *Salix fragilis*), but few species can cope with changing climatic conditions and new sanctuaries appear (Fig. 4, e.g. *P. padus*, *P. alba*, *P. nigra*).

Discussion

Change between current and future predicted habitat

Models predicting the current and future habitat of plants within the typical floodplain forest of the lowland (*Salicion albae*) and the later successional stage floodplain forest (*Fraxinion*) reveal that a majority of habitats is predicted along the main rivers (Rhine, Rhone, Ticino) in Switzerland (Figs. 1 and 4). Still, our study revealed that already under current climatic conditions, only few areas were predicted for all *Salicion albae* species and for a majority of the *Fraxinion* species (Fig. 1). The ecological differences for each species' niches are reflected in the modelled predictions: e.g. the largest *Carex* species of Switzerland, *C. pendula*, revealed a broad distribution reflecting the species' ability to occur also in secondary habitat along forests in wet patches (Lauber 2018). Contrary to that, *C. strigosa* shows limited habitat availability, emphasizing that species of the same genus have different ecological traits and different occurrence potential. Therefore, predictions for landscape and conservation planning should focus on single target species both at the national level as well as at the catchment level (Reichert et al. 2007; Guisan et al. 2013).

The habitat availability of species of both floodplain forest plant communities is predicted to change dramatically both under the moderate and the extreme climate change scenarios, similar to results of other riparian plant species in Switzerland (Fink and Scheidegger 2018) and worldwide (Ikeda et al. 2014) as well as other riparian organisms (D'Amen et al. 2011). Given that the plant community *Salicion albae* is endangered in Switzerland (Delarze et al. 2013; Delarze and Gonseth 2015), the change in habitat availability is important for landscape and conservation planning. Species of the genus *Salix* are predicted to be more flexible towards changing temperature and precipitation patterns, and even show more suitable habitats in the future. The model predictions are overlapping with ecological information, as *Salix* species can occupy secondary habitat and cope with longer dry periods than other species (Chmelar and Meusel 1979; Neumann 1981; Kuzovkina et al. 2004; Francis et al. 2005). Additionally, their potential to survive even extreme conditions has also been found

in a previous study (Fink and Scheidegger 2018; but see in Ikeda et al. 2014).

While the predicted suitable habitat increased for most *Salicion albae* species, there was still a shift in catchments providing modelled suitable habitat, e.g. for *S. purpurea* (from Rhine to Ticino catchment) and *S. myrsinifolia* (from Rhine to Inn catchment, see Figure A2). This information is valuable as conservation and landscape planning strategies frequently focus on the catchment level. Additional change in future habitat availability might be due to extreme water table changes and flooding, which might have an effect on some *Salix* as well as other softwood floodplain forest species in close river proximity (Kuzovkina et al. 2004; Francis et al. 2005). While future models certainly need to consider such information, the climatic, topographic and geological predictors of this study already provide key information on which areas are unsuitable independent of river dynamics and river morphology.

For the species of the *Fraxinion* plant community, the predictions reveal very few habitats as suitable under both climate change scenarios (see Figure A2 for individual species). This is especially crucial as *Fraxinion* habitats are biodiversity hotspots but have long regeneration times (50 to 200 years, see in Werth et al. 2012; Delarze and Gonseth 2015). Additionally, these habitats are already fragmented now (Delarze and Gonseth 2015), and loss of additional suitable sites might further accelerate the loss of some of its vulnerable plant members. Increasing temperatures are likely enhancing the succession of floodplain forests to deciduous forest by lack of moisture (Lang et al. 2014; Delarze and Gonseth 2015). Given that *Fraxinion* floodplain forests are only occasionally flooded and that the overflow is mainly providing fine sediments (Ellenberg 2010), future extreme floods transporting also larger sediments might change the composition of the plant community considerably. Moreover, as most species have limited dispersal abilities (Table 1), conservation planning requires to link dispersal and habitat suitability information to provide target areas for sanctuaries for plant communities (Engler et al. 2009).

Dispersal simulation under climate change assumptions

The presented approach allows to explore various future scenarios to reveal the main driver of species loss by implementing information on dispersal as well as different changes in climate conditions (Engler and Guisan 2009; Engler et al. 2009). Dispersal is more important in structuring metacommunities than environmental processes in high mountain streams (Dong et al. 2016), which is also visible in the spatially explicit output of the simulations for the floodplain forest species investigated here (Fig. 4). While many habitats are suitable (compare Figure A2), the dispersal limitations as well as the information on life history traits implemented in the simulation process limit the spread of the species. Within each plant community group, dispersal vectors varied (see Table 1), but while species which are only dispersed by gravity indeed showed the smallest spread (*Myosoton aquaticum* and *S. officinale*, both within *Salicion albae*, see Fig. 4), high differences were found between wind dispersed species. The spread of various *Carex* species was simulated under similar assumptions, but *C. strigosa* was the least successful colonizer under extreme climate change scenarios of all *Carex* species (Fig. 4). This fact was not due to lower initial presence points used in the simulation, as both *C. strigosa* and *C. brizoides* showed comparable starting points for dispersal simulation (see Table 2), but due to differences in habitat suitability.

Another important point to consider in the interpretation of the results of the simulation are the changes in habitat suitability between various periods in the future, as seen in the analysis on suitable, but not colonized cells (Fig. 2). There, the pattern at each catchment level is more complex than simple dispersal limitations, as not all species showed more cells not being colonized when considering shorter time periods (50 instead of 80 years of dispersal, see Fig. 3). This is in agreement with changing habitat suitability predictions for each catchment between various time periods for several species (see Figure A3, e.g. *C. strigosa*, habitat suitability for Ticino catchment, and compare to Fig. 2, Ticino catchment). Conservation planning is usually done at the catchment level, making information on predicted changes important, especially as riparian species form metacommunities along

catchments (Patrick et al. 2014; Werth and Scheidegger 2014).

While at the plant community level differences between climate change scenarios where significant in terms of colonized cells after 50 and 80 years of dispersal, the significant difference were no longer detected at the individual species level (for softwood floodplain forest species mainly, see results). The individual species were therefore either able to cope with changing climate per se (moderate or extreme), or not able to colonize cells in the future. To predict the outcome of target species for conservation planning, forecasts need be based on individual species' life history and dispersal traits, with a lower focus on changes in habitat suitability due to various climate change scenarios. This is particularly important for restoration projects with post-restoration success control studies, as the prediction using the method presented here allows to distinguish more resilient and vulnerable species.

In our study, some plant species clearly reveal the potential to colonize many areas along catchments in Switzerland, even under extreme climate change scenarios (e.g. *P. alba*, *P. padus*, *S. dulcamara*, see Fig. 4). These species are all considered to be generalists and have a IUCN criteria conservation status of least concern (Delarze and Gonseth 2015), while the species for both softwood and hardwood floodplain forest which are threatened are the least successful also under future climate change scenarios (*E. rhodanensis*, conservation status vulnerable; *M. monophyllos*, conservation status vulnerable; *U. laevis*, conservation status endangered). Especially for these vulnerable species, future sanctuaries are crucial for conservation success.

Floodplains of National Importance and future refugial areas

Functional floodplains should consist of a mosaic of habitats, allowing different plant communities to co-occur in close proximity (Naiman et al. 2005; Ellenberg 2010). Our study reveals that Floodplains of National Importance are not exclusive sanctuaries for floodplain forest species in Switzerland, as for a majority of the plant species less than half of the cells within the designated areas are predicted to harbor these characteristic species (Fig. 3).

The percentage of cells remaining occupied or being colonized in the future within these protected areas further decreases both under moderate and extreme climate change scenarios (Fig. 3). Still, the current protected floodplains might be – or might even become—of importance for other species. Similar shifts have been found for other riparian species in Switzerland (e. g. marginalized habitat for endangered *Myricaria germanica* and *Salix daphnoides*, see in Fink and Scheidegger 2018) and for other plant species in other parts of the world, where only low percentages of currently protected areas are refugia under climate change (Grahama et al. 2019; Hoffmann et al. 2019). This method therefore reveals the potential to plan new target areas for riparian plant conservation in Switzerland, both under changing climate as well as dispersal and life history traits (see also Ikeda et al. 2014; Fink and Scheidegger 2018).

The spatial distribution of current and future available habitat (Fig. 4) stresses the importance of connectivity of sanctuaries along river catchments: Given the frequent dependence on wet areas for germination (Schutz 1997; Ludewig et al. 2014; Sameel et al. 2014), riparian plant species can only establish along a relatively small corridor along rivers, and the spread of species is moderate due to limited dispersal abilities (Andersson et al. 2000; Boedeltje et al. 2003). Additionally, especially plants of the *Salicion albae* community need frequent sediment turnover allowing them to persist despite high competition on gravel bars (Ellenberg 2010). Conservation planning therefore needs to focus on establishing connected sanctuaries areas allowing species survival both under changing climate as well as changing river dynamics.

Limitations of the modelling approach

Species distribution modelling has widely been applied for conservation biology (Guisan et al. 2013), even for rare species (Breiner et al. 2015). Nevertheless, modelling output is highly dependent on data accuracy as well as choice of environmental predictors and modelling method (Franklin 2013), and therefore precautions should be taken. In this study, we used a data set without real absence data, and therefore applied the method most suitable for this type of data (Phillips et al. 2009; Elith et al. 2011). Environmental predictor choice was based on the

species' ecology (see also in Camathias et al. 2013; Breiner et al. 2015; Fink and Scheidegger 2018). Switzerland covers various diverse biogeographic regions (Wohlgemuth 1996), allowing for predictions of various ecological niches along all the catchments included in the study as well as a wide range of values for the predictor layers.

The scale of the modelling approach is not only crucial for predictor variation, but should also be suitable for conservation and planning actions (Elith and Leathwick 2009). We used predictor layers with 100×100 m resolution, as we investigate mainly low distance dispersers, for which the landscape planning for habitat conservation also depends on local stepping stones (Darby and Sear 2008; Hannah et al. 2014b). By using different plant species to represent each community (e.g. trees, shrubs and herbaceous plants), and by focusing on species with high record abundance in Switzerland, the predicted species ranges allow to draw general conclusions for landscape planning undisturbed by individual species' requirements, e.g. of rare species.

Models help understanding core processes in complex natural settings (Gorban and Roose 2011). Species distribution modelling offers the possibility to predict the fate of habitats given changing climate, and therefore allow for a better landscape planning by taking into account future conditions (Drew et al. 2011). While species distribution models alone have been shown to overestimate conservation potential especially for poor dispersers like plants (van-Loon et al. 2011), coupling with dispersal strategies and also including life history traits allow for more realistic predictions (Engler et al. 2009; Fink and Scheidegger 2018). As results of statistical downscaling of global scale climate models to regional scale can reveal uncertainties in climatic predictions (Laflamme et al. 2016), we used the comparison of two extreme climatic change assumptions (moderate and extreme) and averages of predictions over ten year periods to balance outliers for single years. Still, future analyses need to refine modelling approaches by defining the ecological niche of species more precisely, as e.g. for riparian species, hydrological parameters such as inundation frequency or sediment dynamics are crucial for defining the niche at the smaller scale within the riverscape (Gostner et al. 2017), and also the impact of water-mediated dispersal needs to be assessed (Nilsson et al. 2010).

Conclusions

Coupled models linking dispersal and changing habitat under different future climate conditions show non-persistent refugia for floodplain forest species. Although *Salicion albae* species in general are more likely to cope with predicted changes in the climatic conditions than *Fraxinion* species, there are still shifts in target catchments providing sanctuaries. Planning of protected areas for riparian plant species and communities need to focus on connectivity along rivers in Switzerland, and models can help to plan sites suitable for changes in management or for restoration, to maintain viable source populations in dynamic riverine habitats under changing climate.

Acknowledgements We thank three anonymous reviewers and the editor for comments to improve a previous version of the manuscript. The Swiss data base for plants, www.infoflora.ch, provided information on species occurrence. We acknowledge the World Climate Research Program's Working Group on Regional Climate, and the Working Group on Coupled Modelling, former coordinating body of CORDEX and responsible panel for CMIP5 and the climate modelling groups for producing and making available their model output. Dirk Schmatz provided access to future climatic data downscaled for Switzerland. Funding was provided by the Swiss Federal Offices for the Environment for the project "riverscape – sediment dynamics and connectivity".

Authors' contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Sabine Fink. The first draft of the manuscript was written by Sabine Fink and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding provided by Lib4RI – Library for the Research Institutes within the ETH Domain: Eawag, Empa, PSI & WSL. Funding was provided by the Swiss Federal Offices for the Environment for the project "Riverscape – sediment dynamics and connectivity".

Availability of data and materials The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

Consent for publication All authors approved the manuscript for publication.

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