MODELING THE DISTRIBUTION OF RIVERINE VEGETATION IN REGULATED RIVERS – FROM DYNAMIC TO STATIC EQUILIBRIUM

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THESIS PRESENTED TO OBTAIN THE DOCTOR DEGREE IN RIVER RESTORATION AND MANAGEMENT

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Abstract

While methodological advances in ecosystem modeling reflect the growing recognition in the importance of accounting for dynamic change in river ecosystems, it is also recognized that various forms of regulation measures have completely disrupted its natural dynamics. In this context the underlying research question of this PhD is how river regulation affects the spatial distribution of riverine vegetation (aquatic and riparian) and whether rather simple static models that assume equilibrium between vegetation and environmental factors are adequate tools for its prediction.

In a first step, we presented a systematic, quantitative literature review on models to predict the distribution of riverine vegetation on reach scale and identified research gaps to guide the further development of the thesis. Then, we developed and tested a habitat suitability model for aquatic vegetation based on hydrological variables. We concluded that during artificially stabilized (static) low flows the vegetation is in equilibrium with the physical instream condition and showed how the model can be used to define a flow threshold that reduces the risk of species invasion and proliferation. Further, we reconstructed the historic succession dynamics of a large river floodplain using a dynamic vegetation model and showed that typical regulation measures led to a steady progression of the vegetation communities toward mature phases without regression to younger stages. Finally, we applied different static and dynamic modeling approaches for the distribution of floodplain vegetation to the same study area and concluded from the comparison of their results that due to regulation measures the relevance of succession dynamics and disturbance stochasticity for the prediction of vegetation patterns is much reduced.

Consequently, from a river manager´s perspective, static models seem to be an adequate option for the modeling of the distribution of riverine vegetation in artificially stabilized environments since they show high accuracy, need relatively few resources (data, time, expert knowledge) when compared to dynamic models and are reproducible.

Keywords: riparian vegetation, aquatic vegetation, modeling, spatial distribution, river restoration

Resumo

Embora os avanços metodológicos na modelação de ecossistemas reflitam um crescente reconhecimento na importância de processos dinâmicos, reconhece-se também que várias formas de regularização impedem as dinâmicas naturais em muitos rios. Neste contexto, a questão de investigação deste doutoramento é como a regulação dos rios afeta a distribuição espacial da vegetação ribeirinha (aquática e riparia) e se modelos estáticas relativamente simples que assumem equilíbrio entre a vegetação e os fatores ambientais são instrumentos adequados para a sua previsão.

Num primeiro passo, apresentámos uma revisão sistemática e quantitativa de literatura sobre modelos de distribuição de vegetação aquática e ripícola e identificamos lacunas de investigação para orientar o desenvolvimento da tese. Depois, desenvolvemos e testámos um modelo de adequação de habitat para a vegetação aquática com base em variáveis hidrológicas. Concluímos que durante a época vegetativa com caudais artificialmente estabilizados a vegetação está em equilíbrio com as condições hidrológicas e mostrámos como o modelo pode ser usado para a definição de caudais mínimos com o objetivo de reduzir o risco de proliferação por espécies invasoras. Além disso, reconstruímos a sucessão histórica da vegetação ripícola de um grande rio usando um modelo de vegetação dinâmico. Mostrámos que as medidas de regulação causaram uma progressão constante das comunidades de vegetação para fases maduras sem regressão a fases mais jovens. Por último, aplicámos diferentes abordagens de modelação estática e dinâmica para a distribuição da vegetação ripícola para a mesma área de estudo que nos ajudou a concluir, a partir da comparação dos seus resultados, que devido às medidas de regulação a estocasticidade das perturbações fluviais já não é um parâmetro relevante.

Consequentemente concluímos que em ambientes artificialmente estabilizados os modelos estáticos parecem ser uma opção adequada para a modelação da distribuição da vegetação ribeirinha, uma vez que mostram alta precisão, precisam de relativamente poucos recursos (dados, tempo, conhecimento especializado) quando comparados com modelos dinâmicos e ainda são reprodutíveis

Palavras chaves: vegetação riparia, vegetação aquatica, modelos, distribuição espacial, recuperação de rios

Resumo alargado

Para a gestão e recuperação de ecossistemas fluviais é fundamental compreender e prever a distribuição da sua vegetação. Modelos ecológicos podem ajudar neste fim porque permitem testar hipóteses relativas ao funcionamento do ecossistema, a definição de referências ecológicas para projetos de recuperação e previsões dos impactos ecológicos resultantes de cenários de gestão alternativa ou alterações no ambiente. A previsão da distribuição da vegetação de sistemas fluviais naturais com modelos estáticos que presumem um equilíbrio entre a vegetação e fatores ambientais não parece adequada devido às dinâmicas causadas por perturbações hidro-geomorfológicas. Pelo contrário, tem-se teorizado um equilíbrio dinâmico em que processos de progressão são compensados por processos de regressão resultando em proporções constantes de diferentes habitats. Embora os avanços metodológicos na modelação de ecossistemas reflitam um crescente reconhecimento na importância de processos dinâmicos, reconhece-se também que várias formas de regularização impedem completamente as dinâmicas naturais em muitos rios. Neste contexto, a questão de investigação deste doutoramento é a forma como a regulação dos rios afeta a distribuição espacial da vegetação ribeirinha (aquática e riparia) e se modelos estáticas relativamente simples que assumem equilíbrio entre a vegetação e os fatores ambientais são instrumentos adequados para a sua previsão.

O Capítulo 2 é uma revisão sistemática e quantitativa da literatura em revistas de língua inglesa sobre modelos para prever a distribuição da vegetação ribeirinha (aquática e riparia). Foi realizado com o objetivo de dar um panorama abrangente dos modelos existentes e identificar lacunas de investigação para orientar o desenvolvimento da tese. Foram encontradas 41 publicações em revistas de língua inglesa. Através de uma avaliação sistemática destas publicações, poderíamos mostrar que o número de modelos para prever a distribuição da vegetação ribeirinha está a aumentar em todo o mundo, mas que a investigação atual está desproporcionadamente focada na vegetação riparia (>90%) e para rios em nações desenvolvidas do hemisfério norte (>90%). Também, um terço de todos os modelos baseiam-se no pressuposto do equilíbrio entre fatores ambientais e distribuição de vegetação, apesar do reconhecimento da importância da dinâmica da perturbação fluvial. Poucos modelos consideraram a simulação dos processos sucessão (4), competição (5) bem

como os feedbacks entre a hidro-geomorfológia e a vegetação (2). Menos de 10% de todos os modelos foram validados contra dados independentes espaciais.

O capítulo 3 é uma reação a uma das lacunas de investigação diagnosticadas e quer contribuir para a questão de investigação da tese através do desenvolvimento e teste de um modelo espacial de adequação de habitat baseado em variáveis hidrológicas para estudar o efeito de caudais artificialmente estabilizados (estáticos) durante o período de vegetação sobre a vegetação aquática. Os rios mediterrânicos em bacias agrícolas intensivas geralmente exibem crescimento excessivo de vegetação aquática – nomeadamente espécies exóticas – devido a uma combinação de elevadas concentrações de nutrientes e caudais baixos e estabilizados resultantes da abstração da água para a agricultura. Embora a elevada sensibilidade da vegetação aquática às condições hidráulicas seja bem conhecida, as abordagens de gestão baseadas na gestão de caudais permanecem relativamente inexploradas. O objetivo do nosso estudo foi, por isso, aplicar as técnicas de simulação de adequação de habitat promovidas pela "Instream Flow Incremental Method (IFIM)" a vegetação aquática – a primeira vez que foi aplicado neste contexto – de forma a modelar mudanças na adequação do habitat em diferentes cenários de caudal mínimo no rio Sorraia, no centro de Portugal. Usamos 960 pontos de pesquisa distribuídos aleatoriamente para analisar a adequação do habitat relativo aos parâmetros físicos 'velocidade de agua', 'profundidade de água' e 'tamanho do substrato' para as espécies aquáticas mais importantes incluindo *Sparganium erectum* and *Potamogeton crispus e* a invasora *Myriophyllum aquaticum.* Os nossos resultados mostram que o crescimento e a distribuição de macrophytes no período de vegetação hidrologicamente estável estão em equilíbrio com as condições físicas locais. Também foi possível determinar um caudal anual mínimo que poderia impedir o crescimento excessivo e a invasão por *Myriophyllum aquaticum*.

O capítulo 4 tinha como objetivo investigar os efeitos da redução das perturbações hidro-geomorfológicas que a maioria dos grandes rios europeus sofreu durante os últimos séculos na trajetória de sucessão da vegetação riparia. Para estudar estes efeitos e criar um mapa de referência para projetos de recuperação, calibramos e aplicamos um modelo dinâmico de vegetação para reconstruir a dinâmica de sucessão da vegetação riparia de um segmento do rio Reno desde pouco depois de ter sido canalizado (1872) até hoje (2016). A calibração do modelo baseou-se em mapas e dados hidrológicos históricos. A nossa simulação demonstrou uma progressão constante e unilateral das comunidades de vegetação para fases maduras sem regressão a fases mais jovens. Foi possível atribuir este desenvolvimento à falta de perturbações morfodinâmicas suficientemente fortes para repor a sucessão e identificar o stress fisiológico causado por longos períodos de inundação como o fator de controlo mais relevante para a sucessão. A distribuição da vegetação resultante do nosso modelo (2016) pode ser considerada uma estimativa da vegetação natural potencial (PNV). A nossa abordagem tem a grande vantagem sobre a abordagem tradicional para definir a vegetação natural potencial que permite analisar diferentes pontos no tempo, bem como ser abrangente e reprodutível.

A tese culmina no capítulo 5, onde nós, com base nas observações dos capítulos 2, 3 e 4, abordamos diretamente a questão de investigação principal de saber como a regulação dos rios afeta a distribuição espacial da vegetação ribeirinha e se modelos estáticas relativamente simples que assumem equilíbrio entre a vegetação e os fatores ambientais são instrumentos adequados para a sua previsão. Para responder, comparámos os resultados da simulação da sucessão da vegetação do capítulo 4 a diferentes abordagens de modelação estatística para a distribuição da vegetação riparia e discutimo-los no que diz respeito ao conceito de PNV. A validação dos diferentes métodos de estimativa do PNV contra dados independentes e a comparação direta dos seus resultados revelaram desempenhos muito semelhantes. Por conseguinte, concluímos que, devido à falta de grandes perturbações, a vegetação de grandes rios regulamentados atingiu, de facto, um estado de quase equilíbrio com o regime hidrológico alterado e que uma perceção estática da sua PNV parece razoável.

Consequentemente, do ponto de vista de um gestor, em ambientes artificialmente estabilizados, como o rio Sorraia em Portugal (capítulo 3) ou o rio Reno na Alemanha (capítulo 4 e 5) os modelos estáticos parecem ser uma opção adequada para a modelação da distribuição da vegetação ribeirinha, uma vez que mostram alta precisão, precisam de relativamente poucos recursos (dados, tempo, conhecimento especializado) quando comparados com modelos dinâmicos e ainda são reprodutíveis.

Durante a investigação de doutoramento foram identificadas outras assuntos relativas à modelação da distribuição da vegetação ribeirinha que merecem atenção: a) extensão da investigação ao hemisfério sul e aos sistemas fluviais de outros biomas que não sejam do clima temperado e mediterrânico, b) desenvolvimento de modelos para a distribuição da vegetação aquática considerando as dinâmicas fluviais, c) compreender melhor os efeito da variabilidade estocástica de caudais e, no que diz respeito à vegetação riparia do fluxo de águas subterrâneas nos processos e padrões de vegetação, d) desenvolvimento de modelos que incorporem os processos de concorrência, facilitação, e as interações diretas da vegetação com processos geomorfológicas (estes processos tornam-se especialmente importantes no contexto das invasões de espécies a que os rios são particularmente propensos) e e) validação independente de modelos contra dados de diferentes regiões geográficas ou períodos de tempo.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS AND ACRONYMS

AUC	Area Under the receiver operating characteristic Curve
BfG	German Federal Institute of Hydrology
CSI	Composite Suitability Index
DEM	Digital Elevation Model
DM	Dynamic Model
DSI	Depth Suitability Index
EC	European Commission
EFP	Established Forest Phase
ESWP	Early Successional Woodland Phase
EU	European Union
GM	Gradient Model
HHS	Hydraulic Habit Suitability
HL	Herb Layer
HP	Herb Phase
HQ10	Discharge with return period of ten years
HSC	Habitat Suitability Curves
IFIM	Instream Flow Incremental Method
IP	Initial Phase
K	kappa coefficient
LiDAR	Light Detection and Ranging o Laser Imaging Detection
LSWP	Late Successional Woodland Phase
m a.s.l	meters above sea level
MQ	Mean Discharge

OA	Overall Accuracy
PNV	Potential Natural Vegetation
PP	Pioneer Phase
PRISMA	Preferred Reporting Items for Systematic Review Recommendations
Q	Discharge
SDM	Species Distribution Model
SL	Shrub Layer
SM	Statistic Model
SP	Shrub Phase
SSI	Substrate Suitability Index
SW	Shallow Water
TL	Tree Layer
TS	Terminal Stage
TSS	True Skill Statistic
VSI	Velocity Suitability Index
WSE	Water Surface Elevations
WUA	Weighted Usable Area

1 INTRODUCTION

1.1 Background information

1.1.1 Riverine Vegetation

Definition

The vegetation of the riverine ecosystem can be divided into aquatic and riparian vegetation. Aquatic vegetation also referred to as macrophytes or hydrophytes grows within the waterway channel and is adapted to permanent inundation and strong hydrogeomorphological disturbances (O’Hare, 2015). Based on the growth form they can be classified as: submerged plants with roots, floating plants with roots, exclusive floating plants, and emergent plants (Den Hartog and Van Der Velde, 1988).

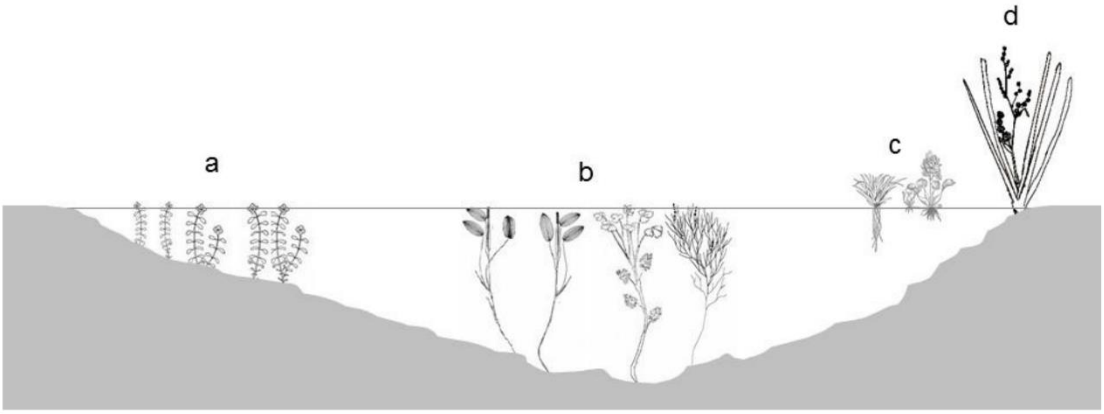

Figure 1: Classification of macrophytes according to their growth form, (a) submerged plants with roots, (b) floating plants with roots, (c) exclusive floating plants, and (d) emergent plants (figure from Schoelynck, 2011)

Another way to group them is based on two distinct strategies to react with the hydrodynamic forces in rivers: avoidance versus tolerance strategy (Puijalon et al., 2011). The avoidance strategists are characterized by high flexibility which allows them to bend with increasing flow velocities thereby reducing the drag force from the flowing water. Macrophytes with the tolerance strategy have less capacity to bend but encounter the higher drag forces they experience through stiff and strong tissue with a high tensile force.

Riparian vegetation is more taxonomically diverse compared with instream macrophytes (O'Hare, 2015). The word “riparian” has its origins in the Latin term “riparius”, meaning what inhabits or belongs to the bank of the river. The riparian ecosystem is found in the transitional zone between aquatic and terrestrial ecosystems. Its spatial extent is normally delineated from the low watermark towards the uplands until the vegetation is not influenced by floods anymore (Naiman and Decamps, 1997). Because of its exposure to hydro-geomorphological disturbances (Formann et al., 2014) it contains plant communities significantly different from those in upland habitats. The riparian zone and their plant communities can be further differentiated based on the dominant fluvial dynamic processes (Gurnell et al., 2016): a) fluvial disturbance dominated zone (coarse sediment erosion and deposition) with riparian and emergent aquatic plants tolerant of frequent inundation, scour and burial b) fluvial disturbance dominated zone (fine sediment deposition) with riparian plants tolerant of regular inundation and moderate sedimentation, c) inundation dominated zone with riparian plants of varying inundation tolerance according to local microtopography, d) soil moisture regime dominated (inundation absent or extremely rare) with plants tolerant of local soil moisture/alluvial groundwater regime.

Importance

Riverine vegetation is an essential part of a functioning river ecosystem (Tabacchi et al., 1998; Allan and Castillo, 2007). Aquatic vegetation influences the biochemical cycles (Allan and Castillo, 2007; Runkel, 2007) and hydraulic condition in the river (O'Hare, 2015). It contributes to the oxygen budget of the water (Caraco et al., 2006) which is essential for the survival of most aquatic organisms (Franklin, 2014) and needed for the decomposition of organic matter (Robarts, 1986). It delivers food and increases the habitat diversity for other water organisms (Woodward and Hildrew, 2002; Thomaz and Cunha, 2010). Also, riparian vegetation provides habitats and nutrients thereby increasing the biodiversity of the river ecosystem (Tabacchi et al., 1998). Riparian vegetation filters pollutants enhancing water quality (Anbumozhi et al., 2005; Dhote and Dixit, 2009), reduce suspended solids creating less turbid water (Jones et al., 2012) and reduce sediment input and pollution from overland flow into the waterway (Chase et al., 2016). Riparian vegetation shades the water, influencing water temperature (Broadmeadow et al., 2011). Both aquatic and riparian vegetation strongly affect the geomorphodynamics of the river system through trapping sediments and stabilizing substrate (Gurnell et al., 2006) and act as ecosystem engineers (Corenblit et al., 2009b; O'Hare et al., 2012). During floods, riparian vegetation reduces surface and channel bank erosion and consequently the potential flood damage (Croke et al., 2017). Another service of riverine vegetation directly valued by human societies is the provision of suitable areas for recreational use (Flather and Cordell, 1995; Holmes et al., 2004).

Pressures

Due to the availability of water, fertile lands and the variety of other ecosystem services fluvial landscapes have been the origin of most early civilizations and urban developments. However, the rise of human societies along riverbanks also caused an impact on the ecosystem, especially since the industrialization (Keddy, 2010).

Anthropogenic land-use of the floodplains and river flow regulation measures have the biggest effect on the riverine ecosystem decline (Tockner and Stanford, 2002; Vörösmarty et al., 2010). It is estimated that 90% of the river floodplains in Europe and North America have been transformed due to agriculture use or forestry (Tockner and Stanford, 2002). The large-scale application of fertilizers and pesticides in combination with other pollution sources such as atmospheric deposition has also resulted in widespread contamination of aquatic ecosystems (Woodward et al., 2012). In addition, the physical environment of the riverine ecosystem has completely changed. Most rivers in North America and Europe are affected by channelization, fragmentation through dams and water regulation resulting from reservoir operation, interbasin diversion, and irrigation (Tockner and Stanford, 2002; Nilsson et al., 2005) which cause an impediment of hydrogeomorphological processes (e.g. avulsion, meandering, braiding) and decrease of hydrodynamic variability (Church, 1995; Kikyo et al., 1999; Magilligan and Nislow, 2005; Petts and Gurnell, 2005).

The combination of altered site conditions with the introduction of species has also caused widespread invasions in riverine ecosystems because they are especially vulnerable due to facilitated transport of propagules, flooding disturbance and water availability (Pysek and Prach, 1993).

The physical habitat of riverine vegetation

The organization and dynamics of both, aquatic and riparian vegetation, in the riverine ecosystem are strongly related to fluvial processes (Poff et al., 1997; Franklin et al., 2008) (Figure 2).

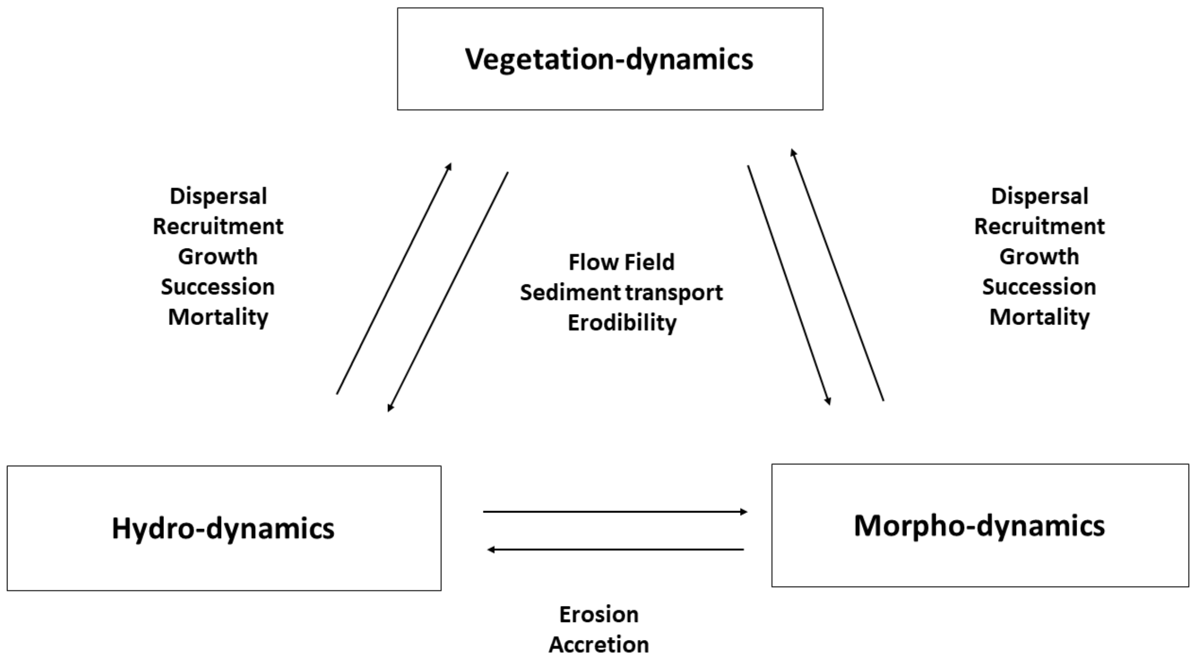

Figure 2: Interaction between fluvial processes and vegetation dynamics (adapted from Corenblit et al., 2007)

Frequency, duration and intensity of flood events determine biomass loss and gain processes of aquatic vegetation (Riis and Biggs, 2003; Franklin et al., 2008). Whereas loss processes are caused by increased drag forces during high flood events that cause steam breakage and uprooting of the plants, biomass gain processes happen in the absence of disturbances during medium to low flow conditions (Riis et al., 2008). Macrophyte dispersal relies mainly on water drift, and thus on seed buoyancy and on the ability of plants to break themselves up and regrow vegetative propagules (Bornette and Puijalon, 2011). Successful colonization of macrophytes is controlled by flood frequency because prolonged periods of hydrological stability are required for macrophyte propagules to settle and develop to substantial levels of cover (Biggs, 1996; Riis and Biggs, 2003; Riis et al., 2008). In these stable interflood periods, macrophyte growth is controlled by several physical and chemical factors, including flow velocity and depth (Chambers et al., 1991; Riis and Biggs, 2003), light availability (Carr et al., 1997; Köhler et al., 2010), water temperature (Barko et al., 1986; Carr et al., 1997), and riverbed grain size (Baattrup-Pedersen and Riis, 1999), as well as the nutrient content of the riverbed and water (Barko et al., 1986; Demars and Edwards, 2009). However it has been argued that water velocity is the main factor in regulating aquatic macrophyte distribution, composition and biomass in rivers (Barko et al., 1986; Chambers et al., 1991; Riis and Biggs, 2003). Normally both the abundance and diversity of macrophytes are stimulated at low to medium velocities, and growth-restricted at higher velocities (Madsen et al., 2001).

Also, riparian vegetation dynamics are strongly influenced by the flow regime (Poff et al., 1997). The external, hydrogeomorphic processes (habitat creation, partial or total destruction of adult vegetation, dispersal of diaspores) and internal processes controlling succession (germination, growth, competition, facilitation) depend primarily on the transverse (from channel to floodplain) hydrogeomorphic disturbance gradient that controls the frequency, duration amplitude and timing of floods and related fluvial processes as a function of the floodplain topography (Junk et al., 1989; Poff et al., 1997; Corenblit et al., 2007).

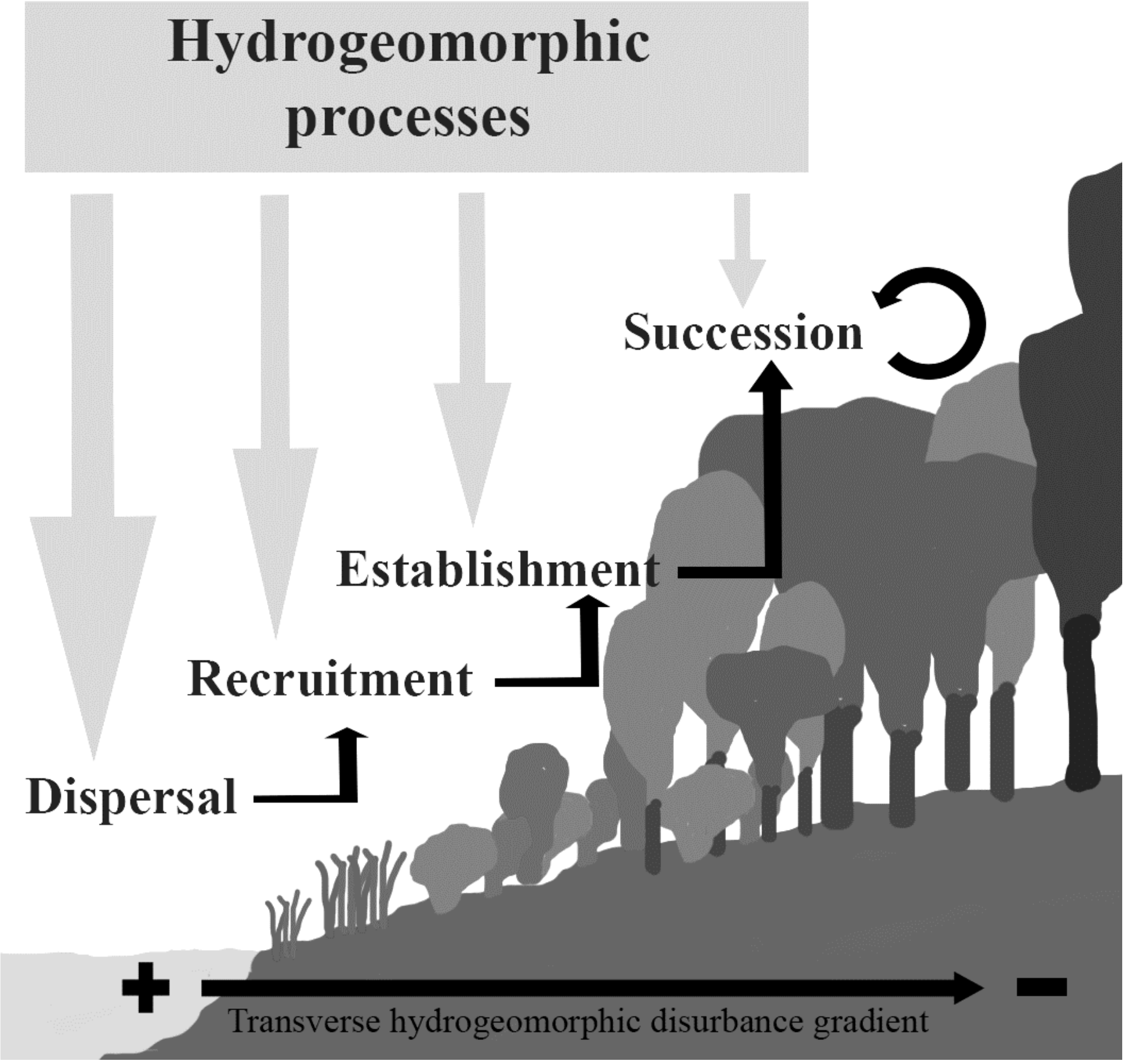

Figure 3: Influence of fluvial processes on vegetation dynamics along the transverse gradient. Gray arrows demonstrate the fluvial control on vegetation processes (size of the arrows indicates the magnitude of the control). Dark arrows demonstrate the time and spatial evolution toward the vegetation succession (adapted from Corenblit et al., 2007)

Plant propagation and dispersal in the riparian corridor are both controlled by floods. During floods, water flow becomes the principal agent of diaspore transport within fluvial corridors, a dissemination process called ‘hydrochory’. Hydro-geomorphological disturbances caused by floods create new possible colonization sites through alluvial deposition and removal of vegetation on pre-existing sites. The deposition of diaspores during the decline of water levels after floods along the alluvial fringe is controlled by floodplain topography and roughness (Andersson et al., 2000; Gurnell et al., 2006).

After dispersal follows the recruitment (germination and seedling survival) phase. Initial vegetation is very sensitive to soil moisture variations (Johnson, 2000). As described in the 'recruitment box model' developed for temperate river systems successful recruitment through seeds is limited to a time window and height band of optimal soil moisture after receding floods (Mahoney and Rood, 1998). The seed release of most riparian species is synchronized with the flow regime (Boedeltje et al., 2004; Stella et al., 2006). Asexual propagation follows a similar trajectory, in which plant parts are ripped off and dragged away by floods and start fixing roots when washed up again on new sites after the flood withdrew (Barsoum, 2001; Boedeltje et al., 2004; Science et al., 2005). Successful recruitment also depends on sediment and organic matter erosion and deposition. On one hand, sediment deposition can provide new colonization sites with optimal conditions of moisture and nutrient for germination and initial plant development (Barsoum, 2001) but it can also inhibit recruitment through burying seedlings. Mobilization of sediments can uproot seedlings and destroy the seed bank (Goodson et al., 2001).

After successful recruitment growth and succession are further controlled by the flow regime. The concept of succession describes the change of vegetation communities over time. Succession usually begins with the disturbance of a pre-existing ecosystem, followed by recovery. In the absence of further disturbance, succession culminates in a stable climax stage (Egger et al., 2013). In the riparian ecosystem the main controlling parameters are flood frequency, duration, intensity and timing (Osterkamp and Hupp, 2010; Formann et al., 2014). Floods cause disturbances through vegetation uprooting, stem breakage and entrainment, burial through sediments or anoxia through flooding (Bendix and Hupp, 2000). Periodic disturbances by floods slow down or reset successional progression. The degree of regression depends on the intensity of the disturbance and the vegetation resistance. The frequency of the disturbance is counterbalanced by the vegetation recovery. Frequency and intensity of the disturbance act as antagonists of vegetation resistance and recovery time which both depend on the life stage and mechanical properties of plant species (Formann et al., 2014).

Riverine vegetation also controls sediment erosion, transport and deposition processes through its resistance to flow and the capacity of its roots to modify substrate erodibility (Nepf and Vivoni, 2000; Gurnell et al., 2006). The impact of vegetation on the sediment dynamics also leads to changes in river morphology (Corenblit et al., 2009b; Gurnell et al., 2012). At the interface between the riparian zone and the low flow channel certain plant species act as physical ecosystem engineers, trapping and stabilizing sediments and plant propagules thereby facilitating plant establishment and colonization by other plant species to build pioneer landforms, which in consequence affects the dynamics of fluvial landforms on large scale (Corenblit et al., 2009a).

1.1.2 Modeling the distribution of riverine vegetation

Ecological models

Ecological models are tools that can help researchers and decision-makers understand ecosystem functioning, improve their knowledge about species distribution, allow predictions of the ecological impacts resulting from alternative management and provide the possibility to define ecological reference (null models) for restoration wherever natural references do not exist (Hannon and Ruth, 1998; Franklin, 2010; Schmolke et al., 2010). Their main advantage when compared to actual physical experiments is that they need less time and financial inputs. In ecological modeling, two fundamentally different approaches may be applied to model species distributions: static models and dynamic models (Hannon and Ruth, 1998).

Static models describe a phenomenon at a given point in time and assume equilibrium between the phenomenon and its environment. Their most basic form are zonation or gradient models, that divide biomes into zones based just one environmental factor, e.g. altitude, latitude, temperature or other biotic factors. Nowadays, the most widely applied type of static models are species distribution models (SDMs) or habitat suitability models

(HSMs), which are statistical tools that associate a given response variable (e.g. the occurrence of a species) with a combination of environmental variables (e.g. temperature, precipitation) (Guisan and Thuiller, 2005). However, the form response and predictor variables are related differs greatly between statistical approaches (Guisan and Zimmermann, 2000). Common model types are Generalised Linear Models (GLM), Generalised Additive Models (GAMS), Neural Networks and machine-learning algorithms such as Boosted Regression Trees (BRT), random forests or the maximum entropy approach (Maxent) (Franklin, 2010). Common methodological issues of statistical models include model and predictor selection (Araújo and Guisan, 2006), spatial autocorrelation (Segurado et al., 2006; Dormann, 2007) as well as collinearity (Dormann et al., 2013) and overfitting (Merow et al., 2014). Additional uncertainty sources that affect all statistical models are data deficiencies (e.g. missing predictors, small sample size) and erroneous model specification (Barry and Elith, 2006). More importantly, several principal assumptions of static models limit their applicability in studies of environmental change (e.g. climate change, environmental flow scenarios) (Guisan and Thuiller, 2005; Araújo and Guisan, 2006). First, they assume equilibrium condition which is violated per se when studying responses to environmental change. Second, they assume the stationarity of estimated statistical relationships across space and time (Miller, 2012) which limits their extrapolation capacity to other regions (Randin et al., 2006) and time (Dobrowski et al., 2010). Also, they are incapable to distinguish between observed absences due to physiological limitation (fundamental niche) and those due to biotic pressure from other species, dispersal limitation or effects of past disturbances (realized niche) (Peterson et al., 2011).

Dynamic models (e.g. process-based models or mechanistic models) are based on ecological processes and differ from static models by explicitly incorporating time-dependent changes in the system state. Therefore they are able to capture the transient response of vegetation to a changing environment (Hannon and Ruth, 2014). For example, transient dynamics, such as succession or recovery from a disturbance that are build on simulations over time in which previous time steps have an impact on the present and future time step. But dynamic models also show certain limitations that distinguish them from static models. They require more ecological information about the modeled species and processes. And they are often more complex therefore requiring more expert knowledge and computational effort than static models. However, if all relevant processes are represented with adequate detail and accuracy, dynamic models are expected to be superior to purely statistical models when applied for extrapolation tasks (Gustafson, 2013).

The dichotomy of the two modeling approaches and their adequate application has also been discussed in more depth by other authors (Peng, 2000; Zurell et al., 2009; Dormann et al., 2012; Gustafson, 2013).

A short history of modeling the distribution of riverine vegetation

Most models to predict the spatial distribution of macrophytes were developed for lentic systems. The first to emerge were gradient approaches linking macrophyte occurrence to water depth (Spence and Chrystal, 1970; Chambers and Kaiff, 1985). With the rising popularity of correlative species distribution models (SDMs) (Guisan et al., 2013) more advanced statistical models were developed considering multiple variables also reflecting the effects of eutrophication (Scheffer et al., 1992; Remillard and Welch, 1993; Lacet et al., 2019). Dynamic approaches were used to model macrophyte growth over time (Titus et al., 1975; Scheffer et al., 1993; Best et al., 2001), but not spatially. Recent dynamic approaches to simulate the spatial growth of macrophytes were cellular automata models (Li et al., 2010; Lin et al., 2011). However, for lotic systems the only models of macrophyte distribution were developed in the last decades and are correlative (Sousa et al., 2009; Spencer and Carruthers, 2013; Zefferman and Harris, 2016; Tinoco et al., 2017).

The first approaches that were developed to explain riparian vegetation patterns were also gradient approaches along vertical (height above channel) and lateral (distance away from channel) gradients (Hosner and Minckler, 1963; Nixon et al., 1977; Robertson et al., 1978; Hughes, 1988; Bowman and Mcdonough, 1991; Glavac et al., 1992; Ward and Stanford, 1995). The next group of models that emerged focused on the distribution of vegetation in response to hydrodynamics, and were usually based on rules that relied on expert knowledge or empiric observations (Lenders et al., 2001; Aggenbach and Pelsma, 2003; Runhaar, 2003; Baptist et al., 2004) or statistical relations (Franz and Bazzaz, 1977; Auble et al., 1994; Menuz, 2011). Process-based models that use a rule system or equations to simulate processes such as growth and mortality, recruitment, succession (progression/retrogression) and competition are a more recent development (Pearlstine et al., 1985; Camporeale and Ridolfi, 2006; Benjankar et al., 2011; García-Arias and Francés, 2016).

The first attempts to incorporate feedbacks from vegetation on hydrodynamics were through quantifying the flow resistance of vegetation in streams. Until today the Manning equation represents the most used resistance measure for vegetated channels (Shields et al., 2017). Different manning's roughness coefficients are normally used to distinguish the flow resistance in the channel from the floodplain in hydrodynamic models (Arcement and Schneider, 1989). However, this approach considers vegetation as a static element that ignores that parameters like vegetation geometry, flow velocity, flow depth and flow regime are dynamic, interacting variables (Horritt and Bates, 2002; Shields et al., 2017). More recently models have been developed that incorporate a more dynamic view of the interaction between vegetation growth and hydrodynamics as well as some feedbacks on sediment transport (Hooke et al., 2005; Camporeale et al., 2013; Bertoldi et al., 2014; Oorschot et al., 2016). But due to the complexity of the involved processes, these models cover only narrow aspects of these interactions (Camporeale et al., 2013; Solari et al., 2016).

1.2 Thesis objectives and outline

Objectives

The modeling of the distribution of vegetation of natural river systems with approaches that assume a static equilibrium between environmental factors and vegetation does not seem reasonable because of the hydro-geomorphological disturbances dynamics (Pringle et al., 1988). On the contrary, a dynamic equilibrium has been theorized in which processes of progression are compensated by regression thereby creating constant habitat proportions on larger scale (Bormann and Likens, 1979; Stanford et al., 2005; Geerling et al., 2006). While methodological advances reflect the growing recognition in the importance of accounting for dynamic change in vegetation modeling, it is also recognized that various forms of river regulation have completely disrupted the natural dynamics in many rivers (Dynesius and Nilsson, 1994; Buijse et al., 2002). In this context and in line with the aims of the doctoral program FLUVIO to contribute to the scientific knowledge about river management and restoration the presented PhD research has the overall objective to explore different modeling approaches that could help river managers to make predictions about the distribution of riverine vegetation in regulated river systems. The underlying research question is how river regulation affects the patterns of aquatic and riparian vegetation and whether the assumption of equilibrium between vegetation and environmental factors inherent of static models can be justified due to the reduction of fluvial dynamics. More specifically the objectives are:

- Identify research gaps in the scientific research on modeling the distribution of riverine vegetation,

and then, in an effort to answer to some of these gaps, as well as contributing the overall research question

- Develop and test a species distribution model to study the effect of regulated, stable minimum flows on the invasion and proliferation of aquatic vegetation,
- Reconstruct the influence of heavy regulation measures on the succession trajectory of riparian vegetation using a dynamic succession model and identify the ecological key processes that control it
- Investigate to which degree the consideration of succession dynamics, time-dependent habitat turnover and fluvial disturbance stochasticity are relevant for the model based prediction of the distribution of riparian vegetation

Outline

As a cumulative dissertation, the body of this thesis consists of four self-contained articles stating the original research carried out to answer the thesis objectives (**chapters 2-5**). They are preceded by an introduction (**chapter 1**) and followed by a final conclusion (**chapter 6**).

Chapter 1 provides the essential background for the understanding of the thesis context and the research performed.

Chapter 2 is a systematic, quantitative literature review in peer-reviewed English speaking journals about the scientific research on modeling the distribution of riverine vegetation on reach scale.

Chapters 3 has been **published in Frontiers in Plant Science.** It is a first-time application of the habitat suitability modeling techniques promoted by the Instream Flow Incremental Method (IFIM) to aquatic macrophytes with the aim to investigate how artificially stabilized summer low flows common for Mediterranean rivers in agricultural watersheds can trigger excessive growth and invasion of aquatic macrophytes.

Chapter 4 has been **published in River Research and Applications**. Based on historical maps and discharge data a dynamic succession model was parameterized to investigate how typical regulations measures of large rivers in the 19th century influenced the succession trajectory of floodplain forests until today.

Chapter 5 has been **published in Hydro-Environment Research.** Through the application of different static and dynamic modeling approaches to the same reach and the comparison of their results it investigates whether the consideration of succession dynamics, time-dependent habitat turnover and fluvial disturbance stochasticity are relevant for the model-based prediction of the distribution of riparian vegetation or whether the assumption of a static equilibrium between vegetation and its hydrological control factors may be justified.

The final **chapter 6** presents the main results, how they relate to the thesis objective and the consequent conclusions of this thesis.

1.3 References

Aggenbach, C. J. S., and Pelsma, T. A. H. M. (2003). Hydro-ecological assessment of vegetation of Dutch river habitats. River Syst. 15, 199–210. doi:10.1127/lr/15/2003/199.

Allan, J. D., and Castillo, M. M. (2007). Stream ecology: structure and function of running waters. doi:10.2307/2265800.

Anbumozhi, V., Radhakrishnan, J., and Yamaji, E. (2005). Impact of riparian buffer zones on water quality and associated management considerations. Ecol. Eng. 24, 517–523. doi:10.1016/j.ecoleng.2004.01.007.

Andersson, E., Nilsson, C., and Johansson, M. E. (2000). Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. J. Biogeogr. 27, 1095–1106.

Araújo, M. B., and Guisan, A. (2006). Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688. doi:10.1111/j.1365-2699.2006.01584.x.

Arcement, G. J., and Schneider, V. R. (1989). Guide for selecting Manning's roughness coefficients for natural channels and flood plains.

Auble, G. T., Friedman, J. M., and Scott, M. L. (1994). Relating Riparian Vegetation to Present and Future Streamflows. Ecol. Appl. 4, 544–554. doi:10.2307/1941956.

Baattrup-Pedersen, A., and Riis, T. (1999). Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. Freshw. Biol. 42, 375–385. doi:10.1046/j.1365-2427.1999.444487.x.

Baptist, M. J., Penning, W. E., Duel, H., Smits, A. J. M., Geerling, G. W., Van der Lee, G. E. M., et al. (2004). Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Res. Appl. 20, 285–297. doi:10.1002/rra.778.

Barko, J. W., Adams, M. S., and Clesceri, N. L. (1986). Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. J. Aquat. Plant Manag. 24, 1–10.

Barry, S., and Elith, J. (2006). Error and uncertainty in habitat models. J. Appl. Ecol. 43, 413–423. doi:10.1111/j.1365-2664.2006.01136.x.

Barsoum, N. (2001). Relative contributions of sexual and asexual regeneration strategies in Populus nigra and Salix alba during the first years of establishment on a braided gravel bed river. Evol. Ecol. 15, 255–279. doi:10.1023/A:1016028730129.

Bendix, J., and Hupp, C. R. (2000). Hydrological and geomorphological impacts on riparian plant communities. Hydrol. Process. 14, 2977–2990. doi:10.1002/1099-1085(200011/12)14:16/17<2977::AID-HYP130>3.0.CO;2-4.

Benjankar, R., Egger, G., Jorde, K., Goodwin, P., and Glenn, N. F. (2011). Dynamic floodplain vegetation model development for the Kootenai River, USA. J. Environ. Manage. 92, 3058–3070. doi:10.1016/j.jenvman.2011.07.017.

Bertoldi, W., Siviglia, A., Tettamanti, S., Toffolon, M., Vetsch, D., and Francalanci, S. (2014). Modeling vegetation controls on fluvial morphological trajectories. Geophys. Res. Lett. 41, 7167–7175. doi:10.1002/2014GL061666.

Best, E. P. H., Buzzelli, C. P., Bartell, S. M., Wetzel, R. L., Boyd, W. A., Doyle, R. D., et al. (2001). Modeling submersed macrophyte growth in relation to underwater light climate: Modeling approaches and application potential. Hydrobiologia 444, 43–70. doi:10.1023/A:1017564632427.

Biggs, B. J. F. (1996). Hydraulic habitat of plants in streams. Regul. Rivers Res. Manag. 12, 131–144. doi:10.1002/(sici)1099-1646(199603)12:2/3<131::aid-rrr385>3.0.co;2-x.

Boedeltje, G. E. R., Bakker, J. A. N. P., Brinke, A. T. E. N., Groenendael, J. A. N. M. V. A. N., and Soesbergen, M. (2004). Dispersal phenology of hydrochorous plants in relation to discharge , seed release time and buoyancy of seeds : the flood pulse concept supported. 786–796.

Bormann, F. H., and Likens, G. E. (1979). Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard Brook ecosystem study. Springer Science & Business Media.

Bornette, G., and Puijalon, S. (2011). Response of aquatic plants to abiotic factors: A review. Aquat. Sci. 73, 1–14. doi:10.1007/s00027-010-0162-7.

Bowman, D. M. J. S., and Mcdonough, L. (1991). Tree Species Distribution across a Seasonally Flooded Elevation Gradient in the Australian Monsoon Tropics. J. Biogeogr. 18, 203–212. doi:Doi 10.2307/2845293.

Broadmeadow, S. B., Jones, J. G., Langford, T. E. L., Shaw, P. J., and Nisbet, T. R. (2011). The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. River Res. Appl. 27, 226–237. doi:10.1002/rra.1354.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., van Geest, G. J., Grift, R. E., et al. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. Freshw. Biol. 47, 889–907. doi:10.1046/j.1365-2427.2002.00915.x.

Camporeale, C., Perucca, E., Ridolfi, L., and Gurnell, A. M. (2013). MODELING THE INTERACTIONS BETWEEN RIVER MORPHODYNAMICS AND RIPARIAN VEGETATION. Rev. Geophys. 51, 379–414. doi:10.1002/rog.20014.

Camporeale, C., and Ridolfi, L. (2006). Riparian vegetation distribution induced by river flow variability: A stochastic approach. Water Resour. Res. 42, n/a-n/a. doi:10.1029/2006WR004933.

Caraco, N., Cole, J., Findlay, S., and Wigand, C. (2006). Vascular Plants as Engineers of Oxygen in Aquatic Systems. Bioscience 56, 219. doi:10.1641/0006-3568(2006)056[0219:vpaeoo]2.0.co;2.

Carr, G. M., Duthie, H. C., and Taylor, W. D. (1997). Models of aquatic plant productivity: a review of the factors that influence growth. Aquat. Bot. 59, 195–215.

Chambers, P. A., and Kaiff, J. (1985). Depth Distribution and Biomass of Submersed Aquatic Macrophyte Communities in Relation to Secchi Depth. Can. J. Fish. Aquat. Sci. 42, 701–709. doi:10.1139/f85-090.

Chambers, P. A., Prepas, E. E., Hamilton, H. R., and Bothwell, M. L. (1991). Current velocity and its effect on aquatic macrophytes in flowing waters. doi:10.2307/1941754.

Chase, J. W., Benoy, G. A., Hann, S. W. R., and Culp, J. M. (2016). Small differences in riparian vegetation significantly reduce land use impacts on stream flow and water quality in small agricultural watersheds. J. Soil Water Conserv. 71, 194–205. doi:10.2489/jswc.71.3.194.

Church, M. (1995). Geomorphic response to river flow regulation: Case studies and time-scales. Regul. Rivers Res. Manag. 11, 3–22. doi:10.1002/rrr.3450110103.

Corenblit, D., Steiger, J., Gurnell, A. M., and Naiman, R. J. (2009a). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: A niche construction perspective for riparian systems. Glob. Ecol. Biogeogr. 18, 507–520. doi:10.1111/j.1466-8238.2009.00461.x.

Corenblit, D., Steiger, J., Gurnell, A. M., Tabacchi, E., and Roques, L. (2009b). Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. Earth Surf. Landforms 34, 1790–1810. doi:10.1002/esp.

Corenblit, D., Tabacchi, E., Steiger, J., and Gurnell, A. M. (2007). Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: A review of complementary approaches. Earth-Science Rev. 84, 56–86. doi:10.1016/j.earscirev.2007.05.004.

Croke, J., Thompson, C., and Fryirs, K. (2017). Prioritising the placement of riparian vegetation to reduce flood risk and end-of-catchment sediment yields : Important considerations in hydrologically-variable regions. J. Environ. Manage. 190, 9–19. doi:10.1016/j.jenvman.2016.12.046.

Demars, B. O. L., and Edwards, A. C. (2009). Distribution of aquatic macrophytes in contrasting river systems: A critique of compositional-based assessment of water quality. Sci. Total Environ. 407, 975–990. doi:10.1016/j.scitotenv.2008.09.012.

Den Hartog, C., and Van Der Velde, G. (1988). “Structural Aspects of Aquatic Plant Communities,” in Vegetation of inland waters, ed. J. J. Symoens (Dordrecht: Springer Netherlands), 113–153. doi:10.1007/978-94-009-3087-2_4.

Dhote, S., and Dixit, S. (2009). Water quality improvement through macrophytes - A review. Environ. Monit. Assess. 152, 149–153. doi:10.1007/s10661-008-0303-9.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M., et al. (2010). Modeling plant distributions over 75 years of measured climate change in California, USA: Relating termporal transferability to species traits. Ecol. Monogr. 81, 241–257.

Dormann, C. F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Glob. Ecol. Biogeogr. 16, 129–138. doi:10.1111/j.1466-8238.2006.00279.x.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). 36, 027–046. doi:10.1111/j.1600-0587.2012.07348.x.

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., et al. (2012). Correlation and process in species distribution models: Bridging a dichotomy. J. Biogeogr. 39, 2119–2131. doi:10.1111/j.1365-2699.2011.02659.x.

Dynesius, M., and Nilsson, C. (1994). Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. Science (80-.). 266, 753–762. doi:10.1126/science.266.5186.753.

Egger, G., Politti, E., Garófano-Gómez, V., Blamauer, B., Ferreira, M. T., Rivaes, R., et al. (2013). "Embodying Interactions Between Riparian Vegetation and Fluvial Hydraulic Processes Within a Dynamic Floodplain Model: Concepts and Applications," in Ecohydraulics: An Integrated Approach, 407–427. doi:10.1002/9781118526576.ch24.

Flather, C. H., and Cordell, H. K. (1995). Outdoor recreation: historical and anticipated trends. Wildl. Recreat. Coexistence through Manag. Res. Isl. Press. Washington, DC, 3–16. Available at:http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Outdoor+recreation+historical+and+anticipated+trends#0.

Formann, E., Egger, G., Hauer, C., and Habersack, H. (2014). Dynamic disturbance regime approach in river restoration: Concept development and application. Landsc. Ecol. Eng. 10, 323–337. doi:10.1007/s11355-013-0228-5.

Franklin, J. (2010). Mapping species distributions. Spatial inference and prediction. Ecol. Biodivers. Conserv. 53, 340. doi:10.1017/CBO9781107415324.004.

Franklin, P. A. (2014). Dissolved oxygen criteria for freshwater fish in New Zealand: A revised approach. New Zeal. J. Mar. Freshw. Res. 48, 112–126. doi:10.1080/00288330.2013.827123.

Franklin, P., Dunbar, M., and Whitehead, P. (2008). Flow controls on lowland river macrophytes: A review. Sci. Total Environ. 400, 369–378. doi:10.1016/j.scitotenv.2008.06.018.

Franz, E. H., and Bazzaz, F. a (1977). Simulation of Vegetation Response to Modified Hydrologic Regimes: A Probabilistic Model Based on Niche Differentiation in a Floodplain Forest. Ecology 58, 176–183. doi:10.2307/1935119.

García-Arias, A., and Francés, F. (2016). The RVDM: modelling impacts, evolution and competition processes to determine riparian vegetation dynamics. Ecohydrology 9, 438–459. doi:10.1002/eco.1648.

Geerling, G. W., Ragas, A. M. J., Leuven, R. S. E. W., van den Berg, J. H., Breedveld, M., Liefhebber, D., et al. (2006). Succession and Rejuvenation in Floodplains along the River Allier (France). Hydrobiologia 565, 71–86. doi:10.1007/s10750-005-1906-6.

Glavac, V., Grillenberger, C., Hakes, W., and Ziezold, H. (1992). On the nature of vegetation boundaries, undisturbed flood plain forest communities as an example - a contribution to the continuum/discontinuum controversy. Vegetatio 101, 123–144. doi:10.1007/BF00033197.

Goodson, J. M., Gurnell, A. M., Angold, P. G., and Morrissey, I. P. (2001). Riparian seed banks: Structure, process and implications for riparian management. Prog. Phys. Geogr. 25, 301–325. doi:10.1177/030913330102500301.

Guisan, A., and Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. Ecol. Lett. 8, 993–1009. doi:10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., et al. (2013). Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. doi:10.1111/ele.12189.

Guisan, A., and Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186. doi:10.1016/S0304-3800(00)00354-9.

Gurnell, A. M., Bertoldi, W., and Corenblit, D. (2012). Changing river channels: The roles of hydrological processes, plants and pioneer fluvial landforms in humid temperate, mixed load, gravel bed rivers. Earth-Science Rev. 111, 129–141. doi:10.1016/j.earscirev.2011.11.005.

Gurnell, A. M., Corenblit, D., García de Jalón, D., González del Tánago, M., Grabowski, R. C., O'Hare, M. T., et al. (2016). A Conceptual Model of Vegetation-hydrogeomorphology Interactions Within River Corridors. River Res. Appl. 32, 142–163. doi:10.1002/rra.2928.

Gurnell, A. M., Morrissey, I. P., Boitsidis, A. J., Bark, T., Clifford, N. J., Petts, G. E., et al. (2006). Initial Adjustments Within a New River Channel: Interactions Between Fluvial Processes, Colonizing Vegetation, and Bank Profile Development. Environ. Manage. 38, 580–596. doi:10.1007/s00267-005-0190-6.

Gustafson, E. J. (2013). When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc. Ecol. 28, 1429–1437. doi:10.1007/s10980-013-9927-4.

Hannon, B., and Ruth, M. (1998). Modeling dynamic biological systems. doi:10.1016/S0898-1221(98)90729-5.

Holmes, T. P., Bergstrom, J. C., Huszar, E., Kask, S. B., and Orr, F. (2004). Contingent valuation, net marginal benefits, and the scale of riparian ecosystem restoration. Ecol. Econ. 49, 19–30. doi:10.1016/j.ecolecon.2003.10.015.

Hooke, J. M., Brookes, C. J., Duane, W., and Mant, J. M. (2005). A simulation model of morphological, vegetation and sediment changes in ephemeral streams. Earth Surf. Process. Landforms 30, 845–866. doi:10.1002/esp.1195.

Horritt, M. S., and Bates, P. D. (2002). Evaluation of 1D and 2D numerical models for predicting river flood inundation. J. Hydrol. 268, 87–99. doi:10.1016/S0022-1694(02)00121-X.

Hosner, J. F., and Minckler, L. S. (1963). Bottomland Hardwood Forests of Southern Illinois--Regeneration and Succession. Ecology 44, 29–41.

Hughes, F. M. R. (1988). The ecology of African floodplain forests in semi-arid and arid zones: a review. J. Biogeogr., 127–140.

Johnson, W. C. (2000). Tree recruitment and survival in rivers: influence of hydrological processes. Hydrol. Process. 14, 3051–3074. doi:10.1002/1099-1085(200011/12)14:16/17<3051::AID-HYP134>3.3.CO;2-T.

Jones, J. I., Collins, A. L., Naden, P. S., and Sear, D. A. (2012). The relationship between fine sediment and macrophytes in rivers. River Res. Appl. 28, 1006–1018. doi:10.1002/rra.1486.

Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. Can. Spec. Publ. Fish. Aquat. Sci. 106, 110–127.

Keddy, P. A. (2010). Wetland ecology: principles and conservation. Cambridge University Press.

Kikyo, M., Tanaka, K., Kamei, T., Ozaki, K., Fujiwara, T., Inoue, E., et al. (1999). An FH domain-containing Bnr1p is a multifunctional protein interacting with a variety of cytoskeletal proteins in Saccharomyces cerevisiae. Oncogene 18, 7046–7054. doi:10.1038/sj.onc.1203184.

Köhler, J., Hachoł, J., and Hilt, S. (2010). Regulation of submersed macrophyte biomass in a temperate lowland river: Interactions between shading by bank vegetation, epiphyton and water turbidity. Aquat. Bot. 92, 129–136. doi:10.1016/j.aquabot.2009.10.018.

Lacet, J. B., Moura, A. do N., and Dantas, Ê. W. (2019). Invasion of Egeria densa Planch. in semiarid reservoirs. Rev. Bras. Bot. 42, 491–497. doi:10.1007/s40415-019-00548-9.

Lenders, H. J. R., Leuven, R. S. E. W., Nienhuis, P. H., de Nooij, R. J. W., and Van Rooij, S. A. M. (2001). BIO-SAFE: a method for evaluation of biodiversity values on the basis of political and legal criteria. Landsc. Urban Plan. 55, 121–137. doi:10.1016/S0169-2046(01)00149-9.

Li, H., Mynett, A., Penning, E., and Qi, H. (2010). Revealing spatial pattern dynamics in aquatic ecosystem modelling with Multi-Agent Systems in Lake Veluwe. Ecol. Inform. 5, 97–107. doi:10.1016/j.ecoinf.2009.08.003.

Lin, Y., Mynett, A., and Li, H. (2011). Unstructured cellular automata for modelling macrophyte dynamics. Int. J. River Basin Manag. 9, 205–210. doi:10.1080/15715124.2011.648732.

Madsen, J. D., Chambers, P. a, James, W. F., Koch, E. W., and Westlake, D. F. (2001). The interaction between water movement, sediment dynamics andsubmersed macrophytes. Hydrobiologia 444, 71–84. doi:10.1023/A:1017520800568.

Magilligan, F. J., and Nislow, K. H. (2005). Changes in hydrologic regime by dams. Geomorphology 71, 61–78. doi:10.1016/j.geomorph.2004.08.017.

Mahoney, J. M., and Rood, S. B. (1998). Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands 18, 634–645.

Menuz, D. R. (2011). Using Species Distribution Models to Assess Invasion Theory and Provide Management Recommendations for Riparian Areas in the Eastern Columbia and Western Missouri River Basins.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., Mcmahon, S. M., Normand, S., et al. (2014). What do we gain from simplicity versus complexity in species distribution models? Ecography (Cop.). 37, 1267–1281. doi:10.1111/ecog.00845.

Miller, J. A. (2012). Species distribution models: Spatial autocorrelation and non-stationarity. Prog. Phys. Geogr. 36, 681–692. doi:10.1177/0309133312442522.

Naiman, R. J., and Decamps, H. (1997). The Ecology of Interfaces: Riparian Zones. Annu. Rev. Ecol. Syst. 28, 621–658.

Nepf, H. M., and Vivoni, E. R. (2000). Flow structure in depth-limited, vegetated flow. J. Geophys. Res. Ocean. 105, 28547–28557. doi:10.1029/2000JC900145.

Nilsson, C., Reidy, C. A., Dynesius, M., and Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. Science (80-.). 308, 405–408. doi:10.1126/science.1107887.

Nixon, E. S., Willett, R. L., and Cox, P. W. (1977). Woody Vegetation of a Virgin Forest in an Eastern Texas River Bottom. Castanea 42, 227–236. Available at: http://www.jstor.org/stable/4032817.

O’Hare, J. M., O’Hare, M. T., Gurnell, A. M., Scarlett, P. M., Liffen, T., and Mcdonald, C. (2012). Influence of an ecosystem engineer, the emergent macrophyte Sparganium erectum, on seed trapping in lowland rivers and consequences for landform colonisation. Freshw. Biol. 57, 104–115. doi:10.1111/j.1365-2427.2011.02701.x.

O’Hare, M. T. (2015). Aquatic vegetation - A primer for hydrodynamic specialists. J. Hydraul. Res. 53, 687–698. doi:10.1080/00221686.2015.1090493.

Oorschot, M. van, Kleinhans, M., Geerling, G., and Middelkoop, H. (2016). Distinct patterns of interaction between vegetation and morphodynamics. Earth Surf. Process. Landforms 41, 791–808. doi:10.1002/esp.3864.

Osterkamp, W. R., and Hupp, C. R. (2010). Fluvial processes and vegetation - Glimpses of the past, the present, and perhaps the future. Geomorphology 116, 274–285. doi:10.1016/j.geomorph.2009.11.018.

Pearlstine, L., McKellar, H., and Kitchens, W. (1985). Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. Ecol. Modell. 29, 283–302. doi:10.1016/0304-3800(85)90057-2.

Peng, C. (2000). From static biogeographical model to dynamic global vegetation model: A global perspective on modelling vegetation dynamics. Ecol. Modell. 135, 33–54. doi:10.1016/S0304-3800(00)00348-3.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., et al. (2011). Ecological Niches and Geographic Distributions (MPB-49). Princeton University Press Available at: http://www.jstor.org/stable/j.ctt7stnh.

Petts, G. E., and Gurnell, A. M. (2005). Dams and geomorphology: Research progress and future directions. Geomorphology 71, 27–47. doi:10.1016/j.geomorph.2004.02.015.

Poff, N. L., Allan, J. D., Bain, M. B., and Karr, J. R. (1997). Natural Flow Regime. Bioscience, 769–784. Available at: http://www.jstor.org/stable/1313099.

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., et al. (1988). Patch Dynamics in Lotic Systems: The Stream as a Mosaic. J. North Am. Benthol. Soc. 7, 503–524. doi:10.2307/1467303.

Puijalon, S., Bouma, T. J., Douady, C. J., van Groenendael, J., Anten, N. P. R., Martel, E., et al. (2011). Plant resistance to mechanical stress: Evidence of an avoidance-tolerance trade-off. New Phytol. 191, 1141–1149. doi:10.1111/j.1469-8137.2011.03763.x.

Pysek, P., and Prach, K. (1993). “Plant invasions and the role of riparian habiats: a comparison of four species alien to central Europe,” in Journal of Biogeography (New York, NY: Springer New York), 413–420. doi:10.2307/2845589.

Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M., and Guisan, A. (2006). Are niche-based species distribution models transferable in space? J. Biogeogr. 33, 1689–1703. doi:10.1111/j.1365-2699.2006.01466.x.

Remillard, M. M., and Welch, R. A. (1993). GIS technologies for aquatic macrophyte studies: Modeling applications. Landsc. Ecol. 8, 163–175. doi:10.1007/BF00125348.

Riis, T., and Biggs, B. J. F. (2003). Hydrologic and hydraulic control of macrophyte establishment and performance in streams. Limnol. Oceanogr. 48, 1488–1497. doi:10.4319/lo.2003.48.4.1488.

Riis, T., Suren, A. M., Clausen, B., and Sand-Jensen, K. (2008). Vegetation and flow regime in lowland streams. Freshw. Biol. 53, 1531–1543. doi:10.1111/j.1365-2427.2008.01987.x.

Robarts, R. D. (1986). Decomposition in freshwater ecosystems. J. Limnol. Soc. South. Africa 12, 72–89. doi:10.1080/03779688.1986.9639399.

Robertson, P. a., Weaver, G. T., and Cavanaugh, J. a. (1978). Vegetation and Tree Species Patterns near the Northern Terminus of the Southern Floodplain Forest. Ecol. Monogr. 48, 249–267.

Runhaar, J. (2003). Natuurgericht landevaluatiesysteem (NATLES) versie 2. Alterra-rapport;550. Available at: http://library.wur.nl/wasp/bestanden/LUWPUBRD_00321225_A502_001.pdf.

Runkel, R. L. (2007). Toward a transport-based analysis of nutrient spiraling and uptake in streams. Limnol. Oceanogr. Methods 5, 50–62. doi:10.4319/lom.2007.5.50.

Scheffer, M., Bakema, A. H., and Wortelboer, F. G. (1993). MEGAPLANT: a simulation model of the dynamics of submerged plants. Aquat. Bot. 45, 341–356. doi:10.1016/0304-3770(93)90033-S.

Scheffer, M., de Redelijkheid, M. R., and Noppert, F. (1992). Distribution and dynamics of submerged vegetation in a chain of shallow eutrophic lakes. Aquat. Bot. 42, 199–216. doi:10.1016/0304-3770(92)90022-B.

Schmolke, A., Thorbek, P., DeAngelis, D. L., and Grimm, V. (2010). Ecological models supporting environmental decision making: A strategy for the future. Trends Ecol. Evol. 25, 479–486. doi:10.1016/j.tree.2010.05.001.

Schoelynck, J. (2011). Macrophyte patches as biogeochemical hotspots: what is the impact on river water quality?. University of Antwerp.

Science, E., Hall, W., Douhovnikoff, V., McBride, J. R., and Dodd, R. S. (2005). Salix exigua clonal growth and population dynamics in relation to disturbance regime variation. Ecology 86, 446–452. doi:10.1890/04-0257.

Segurado, P., Araújo, M. B., and Kunin, W. E. (2006). Consequences of spatial autocorrelation for niche-based models. J. Appl. Ecol. 43, 433–444. doi:10.1111/j.1365-2664.2006.01162.x.

Shields, F. D., Coulton, K. G., and Nepf, H. (2017). Representation of Vegetation in Two-Dimensional Hydrodynamic Models. J. Hydraul. Eng. 143, 02517002. doi:10.1061/(ASCE)HY.1943-7900.0001320.

Solari, L., Van Oorschot, M., Belletti, B., Hendriks, D., Rinaldi, M., and Vargas-Luna, A. (2016). Advances on Modelling Riparian Vegetation-Hydromorphology Interactions. River Res. Appl. 32, 164–178. doi:10.1002/rra.2910.

Sousa, W. T. Z., Thomaz, S. M., Murphy, K. J., Silveira, M. J., and Mormul, R. P. (2009). Environmental predictors of the occurrence of exotic Hydrilla verticillata (L.f.) Royle and native Egeria najas Planch. in a sub-tropical river floodplain: the Upper River Paraná, Brazil. Hydrobiologia 632, 65–78. doi:10.1007/s10750-009-9828-3.

Spence, D. H. N., and Chrystal, J. (1970). Photosynthesis and Zonation of Freshwater Macrophytes: I. Depth Distribution Andshade Tolerance. New Phytol. 69, 205–215. doi:10.1111/j.1469-8137.1970.tb04064.x.

Spencer, D. F., and Carruthers, R. I. (2013). Predicting Eurasian watermilfoil's (Myriophyllum spicatum) distribution and its likely response to biological control in a spring-fed river. J. Aquat. Plant Manag. 51, 7–14.

Stanford, J. A., Lorang, M. S., and Hauer, F. R. (2005). The shifting habitat mosaic of river ecosystems. SIL Proceedings, 1922-2010 29, 123–136. doi:10.1080/03680770.2005.11901979.

Stella, J. C., Battles, J. J., Orr, B. K., and Mcbride, J. R. (2006). Synchrony of Seed Dispersal , Hydrology and Local Climate in a Semi-arid River Reach in California. 1200–1214. doi:10.1007/s10021-005-0138-y.

Tabacchi, E., Correll, D. L., Hauer, R., Pinay, G., Planty-Tabacchi, A. M., and Wissmar, R. C. (1998). Development, maintenance and role of riparian vegetation in the river landscape. Freshw. Biol. 40, 497–516. doi:10.1046/j.1365-2427.1998.00381.x.

Thomaz, S. M., and Cunha, E. R. da (2010). The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnol. Bras. 22, 218–236. doi:10.4322/actalb.02202011.

Tinoco, A. I., Furman, B. T., Darnell, K. M., and Peterson, B. J. (2017). Submerged aquatic vegetation, topography and flow characteristics in the upper, tidal Hudson River: Progress toward a predictive habitat model. Aquat. Bot. 142, 53–60. doi:10.1016/j.aquabot.2017.06.006.

Titus, J., Goldstein, R. A., Adams, M. S., Mankin, J. B., O'Neill, R. V., Weiler, P. R., et al. (1975). A Production Model for Myriophyllum spicatum L. Ecology 56, 1129–1138. doi:10.2307/1936152.

Tockner, K., and Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. Environ. Conserv. 29, 308–330. doi:10.1017/S037689290200022X.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., et al. (2010). Global threats to human water security and river biodiversity. Nature 467, 555–561. doi:10.1038/nature09440.

Ward, J. V., and Stanford, J. A. (1995). Ecosystems and Its Disruption By Flow Regulation. Regul. Rivers Res. Manag. II, 105–119. doi:10.1002/rrr.3450110109.

Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., et al. (2012). Continental-scale effects of nutrient pollution on stream ecosystem functioning. Science (80-.). 336, 1438–1440. doi:10.1126/science.1219534.

Woodward, G., and Hildrew, A. G. (2002). Food web structure in riverine landscapes. Freshw. Biol. 47, 777–798. doi:10.1046/j.1365-2427.2002.00908.x.

Zefferman, E. P., and Harris, D. J. (2016). Predicting drivers of nuisance macrophyte cover in a regulated California stream using boosted regression tree models. J. Aquat. Plant Manag. 54, 78–86.

Zurell, D., Jeltsch, F., Dormann, C. F., and Schröder, B. (2009). Static species distribution models in dynamically changing systems: How good can predictions really be? Ecography (Cop.). 32, 733–744. doi:10.1111/j.1600-0587.2009.05810.x

2 PREDICTING SPATIAL PATTERNS OF RIVERINE VEGETATION: CURRENT LITERATURE AND FUTURE DIRECTIONS

2.1 Abstract

For conservation, restoration and management of the riverine ecosystem it is fundamental to understand and predict the distribution of the its vegetation (aquatic and riparian). Using a systematic, quantitative literature review we identified 41 publications in peer-reviewed English speaking journals where models have been used to help with this task on reach scale. Through a systematic assessment of these publications, we could show that the number of publications and case studies is increasing across the globe but that current research is disproportionately focused on riparian vegetation (>90%) and towards rivers in developed nations of the northern hemisphere (>90%). 31 unique models could be distinguished. Surprisingly one-third were based on the assumption of equilibrium between environmental factors and vegetation distribution despite the recognition of the importance of fluvial disturbance dynamics. Few models considered the simulation the processes succession (4), competition (5) as well as the feedbacks between hydro-morphology and riverine vegetation (2). Less than 10% of all models were validated against spatial independent data. This review provides evidence of important research gaps.

Key words: aquatic vegetation, riparian vegetation, review, model, distribution

2.2 Introduction

Aquatic and riparian vegetation are an essential part of the river ecosystem (Tabacchi et al., 1998; Allan and Castillo, 2007). Their organization and dynamics are both strongly related to the flow regime (Poff et al., 1997; Riis and Biggs, 2003). However, in many rivers various forms of river regulation have completely altered their physical environment (Dynesius and Nilsson, 1994; Buijse et al., 2002). For management, conservation and restoration it is therefore fundamental to understand and predict the spatial pattern of the riverine vegetation (Arthington et al., 2010; Franklin, 2013). Ecological models can help this purpose because they allow the testing of hypothesis regarding the functioning of the ecosystem, the definition of ecological references (null models) for restoration and predictions of the environmental impacts resulting from alternative management scenarios or changes in the environment (Franklin, 2010; Schmolke et al., 2010). Their main advantage when compared to actual physical experiments is that they need less time and financial inputs (Hannon and Ruth, 1998).

In this study we did a systematic, quantitative review of English language papers published in peer-reviewed academic journals about modeling the distribution of riverine vegetation on reach scale to quantitively analyze: (1) the general information of the publication featuring a model, (2) the scope of model application, (3) the different modeling approaches and models, (4) the model parameters and (6) the model validation strategy.

The overall objective is to give a comprehensive overview on where, how and for what reasons the spatial distribution of riverine vegetation has been modeled and what appear to be gaps in the research literature.

2.3 Methodology

The data for this review was retrieved from three databases Web of Science, Scopus and Google Scholar between June and September 2017. Two separate search queries were made, one for publications regarding macrophytes and one for riparian vegetation. Synonyms for model (or “simulation” or “prediction”) and distribution (or “pattern”) and river (or "stream" or "creek") were either combined with synonyms for “aquatic macrophytes” (or “macrophytes” or “aquatic vegetation” or “aquatic plants”) or for “riparian vegetation” (or “riparian forest” or “floodplain forest” or “floodplain vegetation”). Because Google Scholar doesn’t allow for nested searches just the most common terms defining the research topic were combined (macrophytes or “riparian vegetation” with model, distribution and river) and only the first 400 hundred results ordered by relevancy were analyzed.

We followed the protocol developed by the Preferred Reporting Items for Systematic Review Recommendations (PRISMA) (Moher et al., 2015). First titles and journal information were screened to remove duplicates and grey literature (not published in peer-reviewed journals). Then the title, keywords and abstracts and in a second step the full text of the remaining publication were analyzed to remove all publications not describing predictive models of the spatial distribution of single species or species groups at reach/segment scale (1-100 km2, Gurnell et al., 2015) in river systems. Publications belonging to the same model were grouped so that the number of unique models that have been developed as well as the number of model applications and case studies could be counted.

For each eligible publication the basic data on the paper itself, including the year of publication, author(s), and journal title was inserted into a specific database. We distinguished between different research goals: Theoretical ecology, model development, evaluating model implementations, helping design conservation planning strategies, estimating the impact of dam operations and estimating the impact of climate change.

The country, geographical location and biome (Olson et al., 2001) of the study site/s of each model application was entered into the database. We characterized the river systems of the study sites by their catchment size and altitude based on the European river typology (Water Framework Directive 2000/60/EC). The Catchment area was classified in small (10 to 100 km2), medium (100 to 1000 km2), large (1000 to 10 000 km2) and very large (> 10 000 km2). Regarding the altitude the following classes were registered: high (> 800 m), mid-altitude (200 to 800 m) and lowland (< 200 m).

Static or dynamic models were distinguished based on whether they incorporate time-dependent changes in the system state or not (Hannon and Ruth, 1998). Within these two categories different modeling approaches were recognized: Static, expert-based models, correlative models and process-based models either based on equations or rules (Dormann et al., 2012; Peterson et al., 2015). The response variable was classified as being either single species or some kind of species group (e.g. functional types, plant sociological units). The environmental variables affecting vegetation were described through the following categories: chemical and physical water attributes (e.g. turbidity, nutrient content, temperature), chemical and physical soil attributes (e.g. nutrient content, organic matter, texture), meteorological variables (e.g. temperature, photosynthesis active radiation, precipitation), topographic variables (e.g. elevation, distance to channel), variables describing the flow or flood regime (e.g. flood duration, water table) and variables related to the groundwater table. For the process-based models we also registered which vegetation processes were considered: colonization/recruitment, growth, succession, competition, mortality and feedbacks between vegetation and geomorphologic processes (sedimentation/erosion).

Lastly, we assessed whether each unique model had been validated in a case study. We differentiated between 4 validation strategies with increasing robustness (Roberts et al., 2017): no validation at all, validation by resubstitution where calibration equals validation data, validation against hold-out data where a subset of the data (spatial and/or temporal) is retained randomly or manually and validation against truly independent data.

2.4 Results

Overall 41 journal articles in international peer-reviewed journals about modeling the spatial distribution of riverine vegetation on reach scale were identified, 37 regarding riparian vegetation and only four regarding aquatic macrophytes (Figure 4, see Table D1 and D2 for a summary of the complete database). The main reasons for exclusion of a publication from the database were: a) not published in a peer-reviewed journal, b) not about lotic systems, c) model developed for different scale than reach scale, d) not a predictive model and e) model output not spatially distributed.

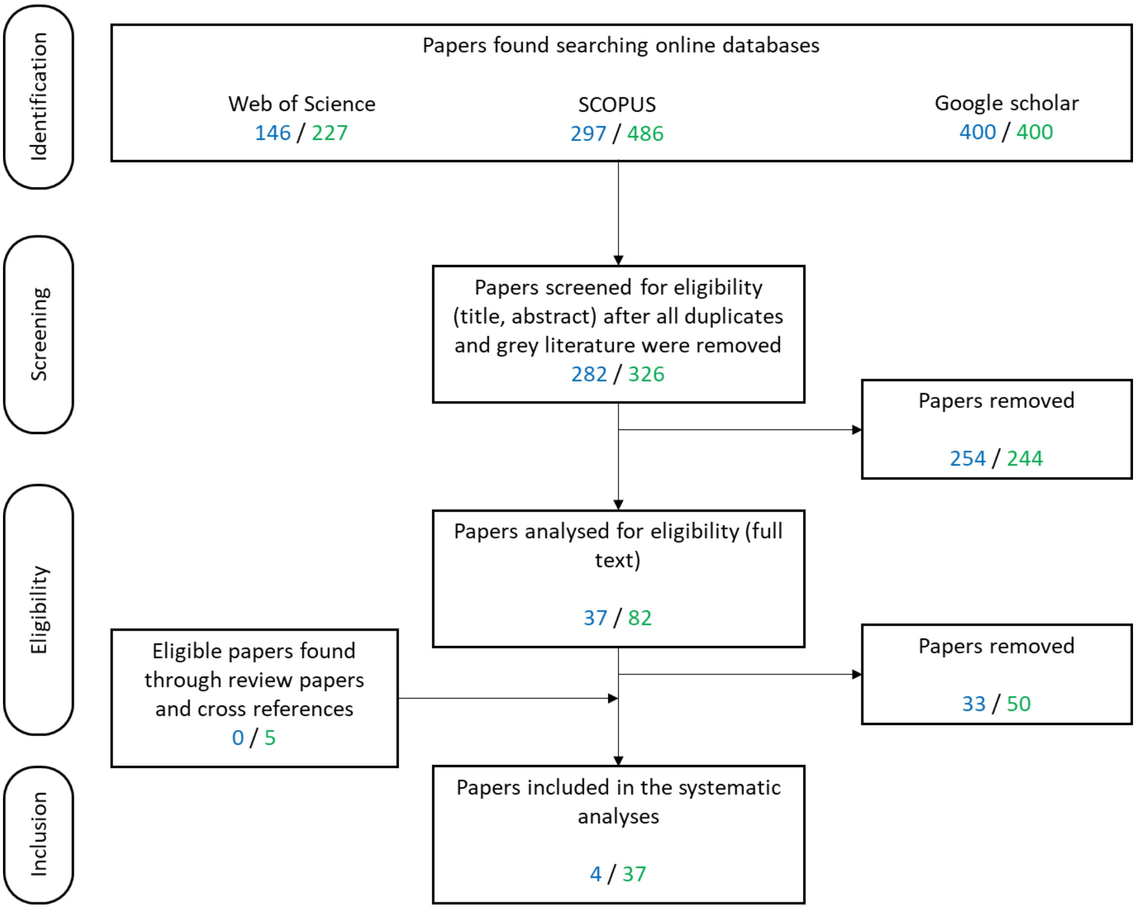

Figure 4: Flowchart outlining the selection process of original research papers following the Preferred Reporting Items for Systematic Review Recommendations (PRISMA). In blue: number papers regarding aquatic macrophytes; in green: papers regarding riparian vegetation

The identified articles were published in 25 different peer-reviewed journals. Only the group of journals with a focus on aquatic science (River Research and Applications, Hydro-environment Research, Ecohydrology, Water Resource Research) stood out with overall twelve publications (Figure 5). An obvious upward trend regarding the number of publications per decade could be observed (Figure 6). Whereas in the 70ies and 80ties only one article was published per decade in the 2010s there were 21. For aquatic vegetation the research goals were divided equally between theoretical ecology and conservation planning. The most common research goal for publications regarding riparian vegetation was "model development" shared by 17 publications (Figure 7). In eight cases the goal was the assessment of the impact of altered hydrologic regimes through dam operations. Other research goals were about the impact of climate change, conservation planning, the testing of ecological theories or the validation of model implementation.

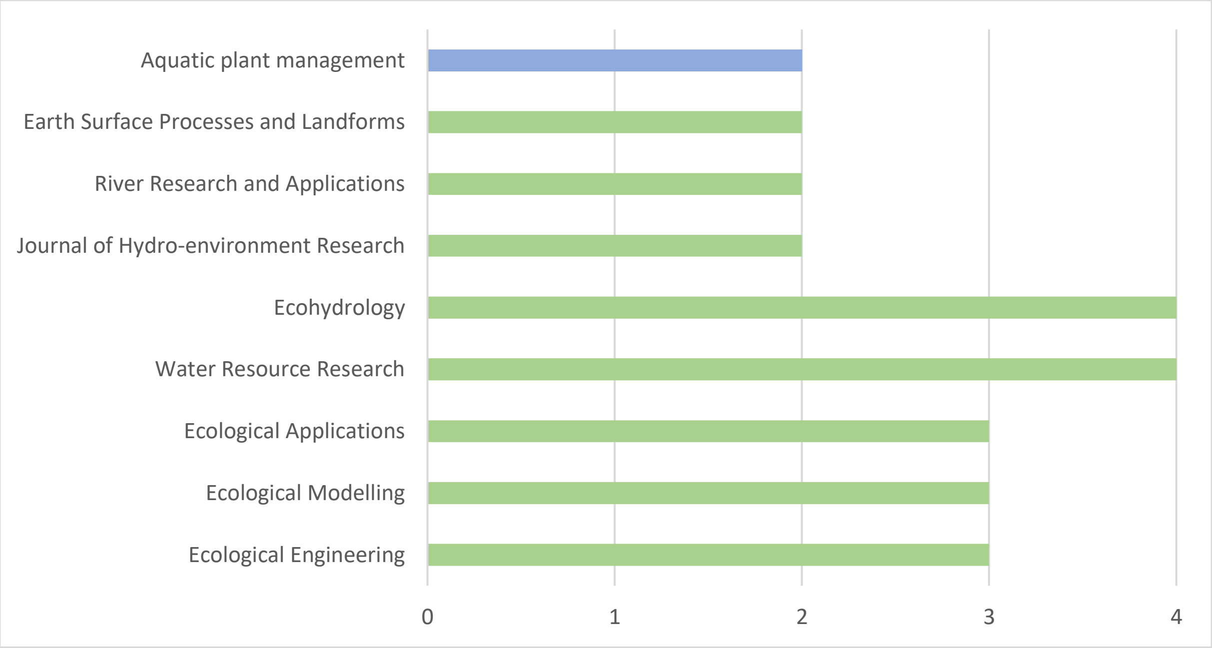

Figure 5: Number of publications (>= 2) regarding the distribution of riverine vegetation per journal (blue: aquatic macrophytes; green: riparian vegetation)

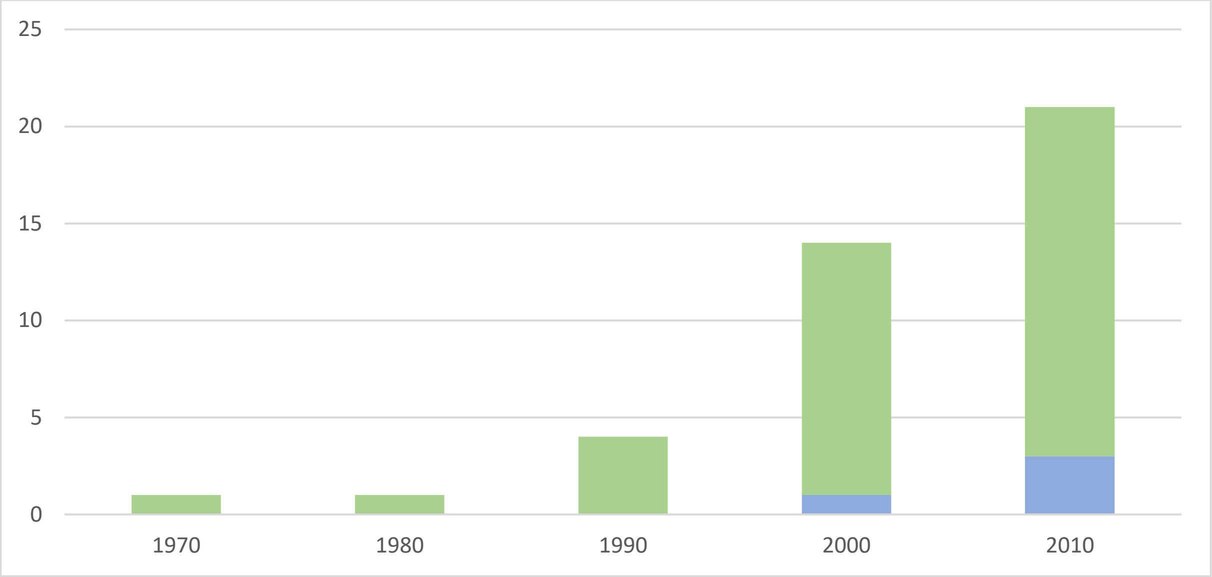

Figure 6: Number of papers per decade (blue: aquatic macrophytes; green: riparian vegetation)

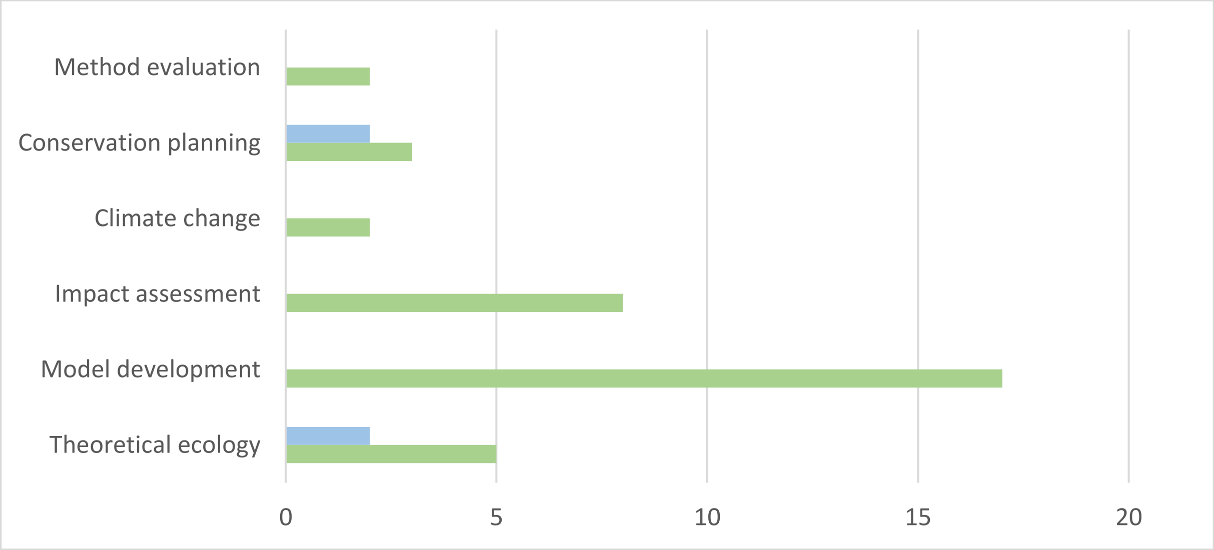

Figure 7: Number of publications per research goal (blue: aquatic macrophytes; green: riparian vegetation)

Geographic scope and characterization of river systems

Concerning aquatic vegetation the four identified publications also presented four independent case studies of model applications in distinct geographic locations (Figure 8): three in North America and one in South America. Four different biomes were represented: temperate broadleaf & mixed forests, mediterranean forests, woodlands & scrub, temperate conifer forests and tropical & subtropical moist broadleaf forests. The study sites ranged from lowland to high altitude rivers. The catchment size of the modeled river systems was large or above. All case studies were affected by flow regulation (Table 1).

For riparian vegetation 37 case studies were counted (Figure 8). Nineteen were found in Europe, ten in Asia and eight in North America. Most models were applied in river systems in temperate broadleaf forests (19). Mediterranean forests counted nine applications, followed by temperate grasslands and savannas with three and deserts and xeric shrublands, temperate conifer forests and subtropical moist broadleaf forest with two applications each. Most of the study sites were in large (11) or very large catchments (17) and lowland rivers (18). The majority of the analyzed river system (34) were regulated and ten study sites were also channelized. Only three model case studies were in free-flowing, not obstructed rivers (Table 1).

A strong bias towards model application in the northern hemisphere could be noticed with only one case study in the southern hemisphere (Figure 8).

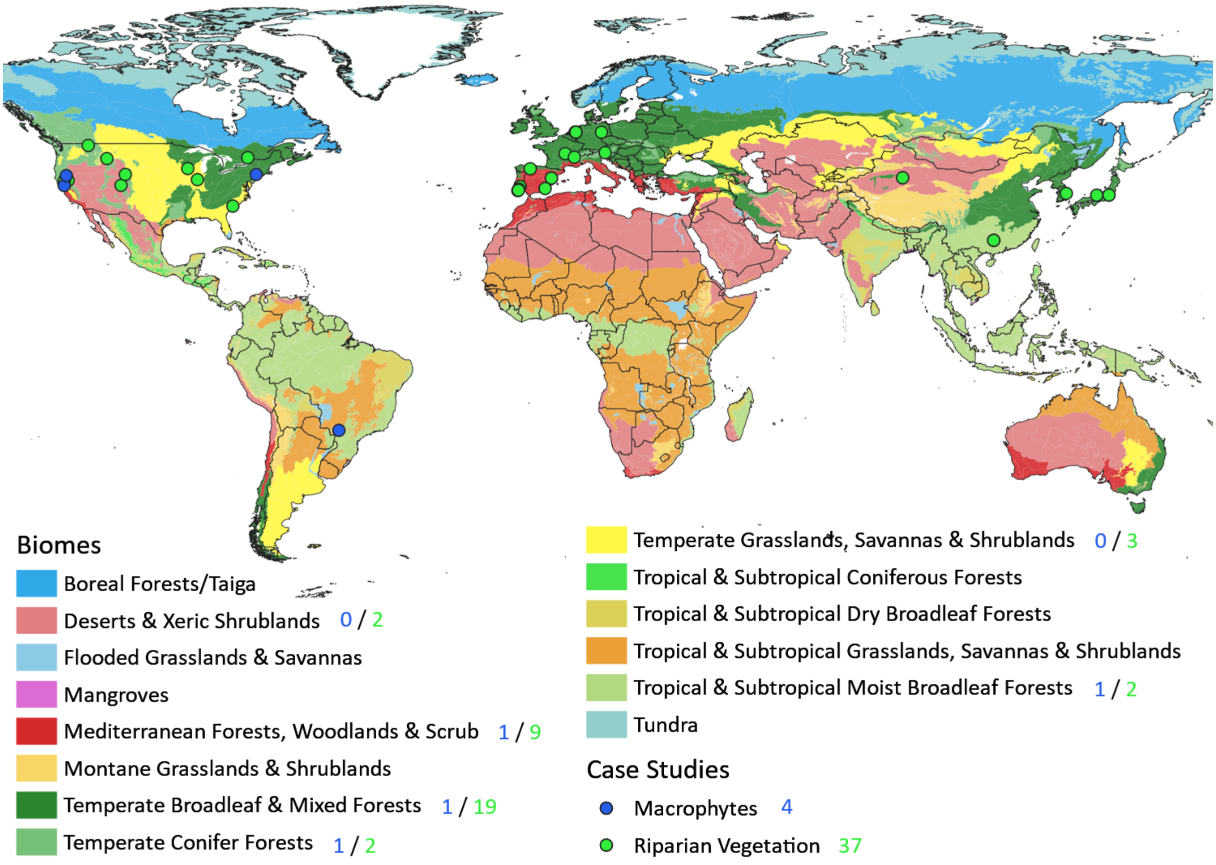

Figure 8: Biomes of the world and the location of model applications for macrophyte and riparian

	Aquatic vegetation	Riparian Vegetation
Catchment size		
Small	-	1
Medium	-	8
Large	2	11
Very large	2	17
Altitude		
Low	1	18

Mid	2	10
High	1	9
Regulation measures		
Flow regulation	4	24
Flow regulation and Channelization	-	10
Free-flowing	-	3

Table 1: Characterization of the river systems of the case studies

Model types and approaches

Four unique models to predict the spatial distribution of macrophytes in river systems were identified (Table 2). All models were correlative approaches. In three cases the response level was single species and in one case a species group (submerged macrophytes). Of the four models three were validated against a hold-out sample, and one was not validated at all.

Within the 37 publications regarding the modeling of riparian vegetation 27 unique models were identified (Table 2). The majority of model types were dynamic (17). Twelve times the processes were described by equations and five times through a set of rules. Static approaches were used in seven cases to predict the spatial distribution of macrophytes within the floodplain, five times statistically and three times by expert knowledge. Most models looked at the distribution of species groups (18) and ten predicted the distribution of single species. From the 27 models eleven were not validated in any case study, seven were validated through resubstitution, five against a hold-out sample and four against independent data.

	Aquatic vegetation	Riparian vegetation
Expert-based (static)	-	**3** (van Ek et al., 2000; Aggenbach and Pelsma, 2003; Benjankar et al., 2014)
Correlative (static)	**4** (Sousa et al., 2009; Spencer and Carruthers, 2013; Zefferman and Harris, 2016; Tinoco et al., 2017)	**7** (Franz and Bazzaz, 1977; Auble et al., 1994; Toner and Keddy, 1997; Chiarello et al., 1998; Hettrich and Rosenzweig, 2003; Hoffman et al., 2008; Ye et al., 2013)
Process-rule-based		**5** (Baptist et al., 2004; Hooke et al., 2005; Benjankar et al., 2011; Harper et al., 2011; Asaeda et al., 2015)
Process-equation-based		**12** (Pearlstine et al., 1985; Hanson et al., 1990; Schaepman et al., 2007; Loheide and Gorelick, 2007; Chen and Ye, 2008; Kooistra et al., 2008; Liu et al., 2012; Perona et al., 2012; Ye et al., 2013; García-Arias et al., 2013; García-Arias and Francés, 2016; Oorschot et al., 2016)

Table 2: Quantitative overview of modeling approaches and unique models (first-time publication). For the complete list of publications see Table D1 and D2

Variables and processes

For the distribution of aquatic vegetation three out of the four models used water attributes as predictors. Soil attributes and the hydrological variables water depth and flow velocity were used by two models (Table 3).

Of the 17 dynamic models regarding riparian vegetation, 14 considered the process of colonization/recruitment and 13 vegetation growth and mortality (Table 3). Five models regarded the succession of plant communities. Six models considered interspecific competition (6). By far the most frequently used variables to explain the distribution of riparian vegetation were hydrological (26). 18 times the variables described aspects of the flow or flood regime and in eight cases the groundwater table. Other variables considered important were topographic (15) and soil related (13).

	Aquatic vegetation	Riparian vegetation
Vegetation processes		
Dispersal	0	2
Colonization/ recruitment	0	14
Growth/mortality	0	14
Succession	0	4
Competition	0	6
Hydrogeomorphological feedbacks	0	2
Environmental Variables		
Soil attributes	2	13
Water attributes	3	0
Climatological	1	2

Topographic	1	14
Hydrological		
Flow/flood regime	2	17
Groundwater regime	0	7

Table 3: Quantitative analyses of different processes and variables used by the models

2.5 Discussion

This systematic quantitative literature review assessed the current literature in English language journals on modeling the spatial distribution of riverine vegetation on reach scale. Thereby it has provided an overview of where and how this task has been accomplished and what appear to be gaps in the research literature. Our focus was on reach scale models because it is the most relevant scale for the majority of river restoration projects (Bernhardt, 2005) and because a similar scale was necessary for the comparison of the modeling approaches and their parameters (Getz et al., 2018).

Our method is based on an approach used in other systematic quantitative literature reviews (Pickering and Byrne, 2014) including species distribution modeling (Robinson et al., 2017). Concentrating on peer-reviewed academic journals enabled us to use a consistent sampling method to detect literature that contains similar levels of detail about the models and complies with standards of research. We note, however, that the identified publications may not reflect the full scope of models. For example, we only included papers written in English as more than 90% of scientific papers are in English (Hamel, 2007). Although our selection included the most common scientific databases (Falagas et al., 2008) we are aware that some models could have been published in journals that are not indexed by them. We also did not include grey literature such as technical manuals or project reports because it is often not publicly available, is written in other language then English and is not included in online searchable databases. Also there can be less consistency in the details provided within grey literature about how research was conducted and data analyzed and the work often have not been subject to peer review.

Few models on the spatial distribution of aquatic vegetation

We found only four papers about modeling the spatial distribution of aquatic vegetation on reach scale as opposed to 37 regarding riparian vegetation. Some models were not included in our data base because they were developed for very large spatial scales like a whole river system, country or continent (e.g. Barendregt and Bio, 2003; Makkay et al., 2008; Rääpysjärvi et al., 2016; Son et al., 2018). However, the vast majority of models for aquatic vegetation that appeared in our search queries were developed for lakes (e.g. Narumalani et al., 1997; Van Den Berg et al., 2003; Vis et al., 2003) or estuaries (e.g. Cerco and Moore, 2001; Kotta et al., 2014). That was surprising because the importance of aquatic vegetation for a functioning river ecosystem is also highly recognized, e.g. in regard to habitat and nutrient provision (Woodward and Hildrew, 2002; Thomaz and Cunha, 2010) or hydro-geomorphological feedbacks (O'Hare, 2015; Gurnell, 2016). Furthermore, because the natural composition and distribution of macrophytes is strongly influenced by anthropogenic disturbances such as eutrophication (Jones et al., 2002; Mainstone and Parr, 2002) and flow regulation (Riis and Biggs, 2003; Franklin et al., 2008) in many rivers excessive growth and species invasion become a management problem (Madsen, 2000; Hussner et al., 2017) and consequently an interesting case for model application. We can only speculate but one reason why fewer models for aquatic vegetation exist could be that the aquatic zone of rivers is less threatened by competing land-use change than the riparian zone. Another reason might be that model calibration and validation data (e.g. aerial photos, field sampling) for aquatic vegetation is more difficult to obtain than compared to riparian vegetation (Vis et al., 2003).

Although much higher, we also found the number of models that fit our criteria to predict riparian vegetation distribution at reach scale unexpectedly low. But some interesting and frequently discussed modeling approaches, such as the models by Camporeale and Ridolfi

(2006), Lytle and Merritt (2004) or Glenz et al. (2008) although contributing to the understanding riparian vegetation response to fluvial processes are not spatially explicit or only at an abstract scale that has limited value as planning basis for applied conservation and restoration projects.

Model application is geographically limited

Model development and applications showed a strong bias towards the northern hemisphere, none for riparian vegetation and only one aquatic vegetation model was counted in the southern hemisphere (Sousa et al., 2009, Brazil). Possible explanations include: (1) fewer researchers and research funding in the countries of the southern hemisphere (Pasgaard and Strange, 2013), (2) the dominance of the English language in academic publishing (Hamel and Metropolitana, 2007; Salager-Meyer, 2008), (3) higher rates of citation/impact for American journals (Anderson-Levitt, 2014) and (4) social biases affecting the perceived importance and quality of research from different regions/languages (Salager-Meyer, 2008; Ferguson et al., 2011).

Static models in dynamic systems

It was surprising that over one-third of the models chose a static approach. Many studies confirm that the spatial patterns of riverine vegetation are an evident indication of its sensitivity to dynamic and stochastic river-induced disturbances (Pringle et al., 1988; Hupp and Osterkamp, 1996; Mahoney and Rood, 1998; Riis et al., 2008; Paice et al., 2016) that constantly rejuvenate and reset successional sequences (Formann et al., 2014). Static models, however, assume equilibrium between the vegetation and its environment (Franklin, 2014). Their suitability for predictions in dynamically changing systems is therefore questionably (Zurell et al., 2009; Dormann et al., 2012). One reason why they are still frequently applied might be that static models in general need less data, know-how and time to be set up (Hannon and Ruth, 1998) and became very popular during the last decade (Guisan et al., 2013). It also raises the question, whether the application of static models could be justified because 90% of all case studies were in regulated rivers with reduced natural dynamics (Nilsson and Berggren, 2000; Magilligan and Nislow, 2005; Petts and Gurnell, 2005).

Neglected processes and variables

Only two out of four aquatic vegetation models predicted the distribution in relation to hydrologic variables even though most research indicates that in rivers macrophyte distribution is also controlled by the hydraulic instream condition (Riis and Biggs, 2003; Franklin et al., 2008; O'Hare, 2015). Also we found none process-based model for aquatic vegetation.

All riparian vegetation models were based on hydrologic variables related to the flow and/or groundwater regime. Less than 30% of riparian vegetation models accounted for the processes of succession or competition in the floodplain although under less disturbed conditions these are considered the dominating processes of vegetation dynamics (Tabacchi et al., 1998; Brooker et al., 2008). The main negative interactions include competition for light, nutrients and water (Brooker et al., 2008). Also, we found only two models that include the simulation of feedbacks between vegetation and geomorphological processes (Hooke et al., 2005; Oorschot et al., 2016) and none include the effects of competition or facilitation combined with morphological development of rivers. Facilitation processes by ecosystem engineers get especially important in the context of invasive species (Tickner et al., 2001) and include reduction of shear stress (Corenblit et al., 2009a), soil enrichment (Brooker et al., 2008), reduction of evaporation by shading, and increasing water infiltration by root systems (Van Noordwijk et al., 2015).

No independent validation

Predictive models are of little value if their outcome is not tested against independent data (Olden et al., 2002; Araújo et al., 2005) for example, from different geographic regions or spatially distinct subsets of the region or different time periods. Only in four cases the model was validated with data from a river reach geographically independent from the calibration reach. More than half of all the models were not validated at all (11) or validated weakly through resubstitution (7) which is an acute violation of non-independence (Roberts et al., 2017). In 5 cases more sophisticated validation procedures were applied that included temporal or geographical data splitting and cross-fitting approaches. These approaches assume that the selected hold out samples from the original data represents sufficiently independent observations for testing. But independence is not guaranteed if calibration and validation data are spatially autocorrelated (Araújo et al., 2005).

Conclusion

The number of models to predict the distribution of riverine vegetation is increasing across the globe. However, there are still very few models regarding aquatic vegetation. Also, current research is disproportionately focused towards rivers in developed nations and temperate and mediterranean habitats of the northern hemisphere. It was surprising that despite the highly dynamic riverine environment one-third of all models are based on the assumption of equilibrium between vegetation and environmental factors. There is also a lack of models incorporating the simulation of processes such as succession, competition and facilitation as well as the feedbacks between hydrogeomorphology and riverine vegetation.

The nature of the applied review technique is to give a quantitative overview of the research topic (Pickering and Byrne, 2014). It should be understood as complementary to existing qualitative reviews that analyze certain aspects of the modeling of riparian vegetation dynamics in greater detail such as hydro geomorphological interactions (Camporeale et al., 2013; Solari et al., 2016), response to flow regulation (Merritt et al., 2010) or other anthropogenic disturbances (You et al., 2015). Together the following future modeling challenges in regard to the distribution of riverine vegetation can be drawn:

- Development of models to predict the distribution of aquatic vegetation
- Extend research to the southern hemisphere and river systems of other biomes than the temperate and mediterranean climate

- Development of models that incorporate the direct interactions of vegetation with morphodynamic processes
- Development of models of vegetation succession and the inclusion of competition and facilitation processes
- Test model reliability through independent validation

2.6 References

Aggenbach, C. J. S., and Pelsma, T. A. H. M. (2003). Hydro-ecological assessment of vegetation of Dutch river habitats. River Syst. 15, 199–210. doi:10.1127/lr/15/2003/199.

Allan, J. D., and Castillo, M. M. (2007). Stream ecology: structure and function of running waters. doi:10.2307/2265800.

Anderson-Levitt, K. (2014). Significance: U.S. Blind Spots in Judging Research. Educ. Policy Anal. Arch. doi:10.14507/epaa.v22n27.2014.

Araújo, M. B., Pearson, R. G., Thuiller, W., and Erhard, M. (2005). Validation of species-climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513. doi:10.1111/j.1365-2486.2005.01000.x.

Arthington, A. H., Naiman, R. J., McClain, M. E., and Nilsson, C. (2010). Preserving the biodiversity and ecological services of rivers: New challenges and research opportunities. Freshw. Biol. 55, 1–16. doi:10.1111/j.1365-2427.2009.02340.x.

Asaeda, T., Rashid, M. H., and Abu Bakar, R. (2015). Dynamic Modelling of Soil Nitrogen Budget and Vegetation Colonization in Sediment Bars of a Regulated River. River Res. Appl. 31, 470–484. doi:10.1002/rra.2802.

Auble, G. T., Friedman, J. M., and Scott, M. L. (1994). Relating Riparian Vegetation to Present and Future Streamflows. Ecol. Appl. 4, 544–554. doi:10.2307/1941956.

Baptist, M. J., Penning, W. E., Duel, H., Smits, A. J. M., Geerling, G. W., Van der Lee, G. E. M., et al. (2004). Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Res. Appl. 20, 285–297. doi:10.1002/rra.778.

Barendregt, A., and Bio, A. M. F. (2003). Relevant variables to predict macrophyte communities in running waters. Ecol. Modell. 160, 205–217. doi:10.1016/S0304-3800(02)00254-5.

Benjankar, R., Egger, G., Jorde, K., Goodwin, P., and Glenn, N. F. (2011). Dynamic floodplain vegetation model development for the Kootenai River, USA. J. Environ. Manage. 92, 3058–3070. doi:10.1016/j.jenvman.2011.07.017.

Benjankar, R. M., Burke, M., Yager, E. M., Tonina, D., Egger, G., Rood, S. B., et al. (2014). Development of a spatially-distributed hydroecological model to simulate cottonwood seedling recruitment along rivers. J. Environ. Manage. 145, 277–288.

Bernhardt, E. S. (2005). ECOLOGY: Synthesizing U.S. River Restoration Efforts. Science (80-.). 308, 636–637. doi:10.1126/science.1109769.

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., et al. (2008). Facilitation in plant communities: The past, the present, and the future. J. Ecol. 96, 18–34. doi:10.1111/j.1365-2745.2007.01295.x.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., van Geest, G. J., Grift, R. E., et al. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. Freshw. Biol. 47, 889–907. doi:10.1046/j.1365-2427.2002.00915.x.

Camporeale, C., Perucca, E., Ridolfi, L., and Gurnell, A. M. (2013). MODELING THE INTERACTIONS BETWEEN RIVER MORPHODYNAMICS AND RIPARIAN VEGETATION. Rev. Geophys. 51, 379–414. doi:10.1002/rog.20014.

Camporeale, C., and Ridolfi, L. (2006). Riparian vegetation distribution induced by river flow variability: A stochastic approach. Water Resour. Res. 42, n/a-n/a. doi:10.1029/2006WR004933.

Cerco, C. F., and Moore, K. (2001). System-Wide Submerged Aquatic Vegetation Model for Chesapeake Bay. Estuaries 24, 522. doi:10.2307/1353254.

Chen, Q., and Ye, F. (2008). “Unstructured Cellular Automata and the Application to Model River Riparian Vegetation Dynamics,” in Cellular Automata (Berlin, Heidelberg: Springer Berlin Heidelberg), 337–344. doi:10.1007/978-3-540-79992-4_43.

Chiarello, E., Amoros, C., Pautou, G., and Jolion, J.-M. (1998). Succession modeling of river floodplain landscapes. Environ. Model. Softw. 13, 75–85. doi:10.1016/S1364-8152(97)00034-0.

Corenblit, D., Steiger, J., Gurnell, A. M., and Naiman, R. J. (2009). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: A niche construction perspective for riparian systems. Glob. Ecol. Biogeogr. 18, 507–520. doi:10.1111/j.1466-8238.2009.00461.x.

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., et al. (2012). Correlation and process in species distribution models: Bridging a dichotomy. J. Biogeogr. 39, 2119–2131. doi:10.1111/j.1365-2699.2011.02659.x.

Dynesius, M., and Nilsson, C. (1994). Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. Science (80-.). 266, 753–762. doi:10.1126/science.266.5186.753.

Falagas, M. E., Pitsouni, E. I., Malietzis, G. A., and Pappas, G. (2008). Comparison of PubMed, Scopus, Web of Science, and Google Scholar: strengths and weaknesses. FASEB J. 22, 338–342. doi:10.1096/fj.07-9492LSF.

Ferguson, G., Pérez-Llantada, C., and Plo, R. (2011). English as an international language of scientific publication: A study of attitudes. World Englishes 30, 41–59. doi:10.1111/j.1467-971X.2010.01656.x.

Formann, E., Egger, G., Hauer, C., and Habersack, H. (2014). Dynamic disturbance regime approach in river restoration: Concept development and application. Landsc. Ecol. Eng. 10, 323–337. doi:10.1007/s11355-013-0228-5.

Franklin, J. (2010). Mapping species distributions. Spatial inference and prediction. Ecol. Biodivers. Conserv. 53, 340. doi:10.1017/CBO9781107415324.004.

Franklin, J. (2013). Species distribution models in conservation biogeography: Developments and challenges. Divers. Distrib. 19, 1217–1223. doi:10.1111/ddi.12125.

Franklin, P. A. (2014). Dissolved oxygen criteria for freshwater fish in New Zealand: A revised approach. New Zeal. J. Mar. Freshw. Res. 48, 112–126. doi:10.1080/00288330.2013.827123.

Franklin, P., Dunbar, M., and Whitehead, P. (2008). Flow controls on lowland river macrophytes: A review. Sci. Total Environ. 400, 369–378. doi:10.1016/j.scitotenv.2008.06.018.

Franz, E. H., and Bazzaz, F. a (1977). Simulation of Vegetation Response to Modified Hydrologic Regimes: A Probabilistic Model Based on Niche Differentiation in a Floodplain Forest. Ecology 58, 176–183. doi:10.2307/1935119.

García-Arias, A., and Francés, F. (2016). The RVDM: modelling impacts, evolution and competition processes to determine riparian vegetation dynamics. Ecohydrology 9, 438–459. doi:10.1002/eco.1648.

García-Arias, A., Francés, F., Morales-de la Cruz, M., Real, J., Vallés-Morán, F., Garófano-Gómez, V., et al. (2013). Riparian evapotranspiration modelling: Model description and implementation for predicting vegetation spatial distribution in semi-arid environments. Ecohydrology 7, n/a-n/a. doi:10.1002/eco.1387.

Getz, W. M., Marshall, C. R., Carlson, C. J., Giuggioli, L., Ryan, S. J., Romañach, S. S., et al. (2018). Making ecological models adequate. Ecol. Lett. 21, 153–166. doi:10.1111/ele.12893.

Glenz, C., Iorgulescu, I., Kienast, F., and Schlaepfer, R. (2008). Modelling the impact of flooding stress on the growth performance of woody species using fuzzy logic. Ecol. Modell. 218, 18–28. doi:10.1016/j.ecolmodel.2008.06.008.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., et al. (2013). Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. doi:10.1111/ele.12189.

Gurnell, A. M. (2016). Hydrogeomorphology- Ecology Interactions in River Systems. River Res. Appl. 22, 1085–1095. doi:10.1002/rra.

Gurnell, A. M., del Tánago, M., Rinaldi, M., Grabowski, R. C., Henshaw, A., O'Hare, M., et al. (2015). "Development and Application of a Multi-scale Process-Based Framework for the Hydromorphological Assessment of European Rivers," in Engineering Geology for Society and Territory - Volume 3: River Basins, Reservoir Sedimentation and Water Resources, eds. G.

Lollino, M. Arattano, M. Rinaldi, O. Giustolisi, J.-C. Marechal, and G. E. Grant (Cham: Springer International Publishing), 339–342. doi:10.1007/978-3-319-09054-2_71.

Hamel, R. E., and Metropolitana, U. A. (2007). The dominance of English in the international scientific periodical literature and the future of language use in science. 20, 53–71. doi:10.1075/aila.20.06ham.

Hannon, B., and Ruth, M. (1998). Modeling dynamic biological systems. doi:10.1016/S0898-1221(98)90729-5.

Hanson, J. S., Malanson, G. P., and Armstrong, M. P. (1990). Landscape fragmentation and dispersal in a model of riparian forest dynamics. Ecol. Modell. 49, 277–296. doi:10.1016/0304-3800(90)90031-B.

Harper, E. B., Stella, J. C., and Fremier, A. K. (2011). Global sensitivity analysis for complex ecological models: a case study of riparian cottonwood population dynamics. Ecol. Appl. 21, 1225–1240. doi:10.1890/10-0506.1.

Hettrich, A., and Rosenzweig, S. (2003). Multivariate statistics as a tool for model-based prediction of floodplain vegetation and fauna. Ecol. Modell. 169, 73–87.

Hoffman, J. D., Narumalani, S., Mishra, D. R., Merani, P., and Wilson, R. G. (2008). Predicting Potential Occurrence and Spread of Invasive Plant Species along the North Platte River, Nebraska. Invasive Plant Sci. Manag. 1, 359–367. doi:10.1614/IPSM-07-048.1.

Hooke, J. M., Brookes, C. J., Duane, W., and Mant, J. M. (2005). A simulation model of morphological, vegetation and sediment changes in ephemeral streams. Earth Surf. Process. Landforms 30, 845–866. doi:10.1002/esp.1195.

Hupp, C. R., and Osterkamp, W. R. (1996). Riparian vegetation and fluvial geomorphic processes. Geomorphology 14, 277–295. doi:10.1016/0169-555X(95)00042-4.

Hussner, A., Stiers, I., Verhofstad, M. J. J. M., Bakker, E. S., Grutters, B. M. C., Haury, J., et al. (2017). Management and control methods of invasive alien freshwater aquatic plants: A review. Aquat. Bot. 136, 112–137. doi:10.1016/j.aquabot.2016.08.002.

Jones, J. I., Young, J. O., Eaton, J. W., and Moss, B. (2002). The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interaction between submerged plants and periphyton. J. Ecol. 90, 12–24. doi:10.1046/j.0022-0477.2001.00620.x.

Kooistra, L., Wamelink, W., Schaepman-Strub, G., Schaepman, M., van Dobben, H., Aduaka, U., et al. (2008). Assessing and predicting biodiversity in a floodplain ecosystem: Assimilation of net primary production derived from imaging spectrometer data into a dynamic vegetation model. Remote Sens. Environ. 112, 2118–2130. doi:10.1016/j.rse.2007.10.010.

Kotta, J., Möller, T., Orav-Kotta, H., and Pärnoja, M. (2014). Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. Mar. Environ. Res. 102, 88–101. doi:10.1016/j.marenvres.2014.05.002.

Liu, D., Tian, F., Hu, H., Lin, M., and Cong, Z. (2012). Ecohydrological evolution model on riparian vegetation in hyperarid regions and its validation in the lower reach of Tarim River. Hydrol. Process. 26, 2049–2060. doi:10.1002/hyp.8313.

Loheide, S. P., and Gorelick, S. M. (2007). Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. Water Resour. Res. 43, 1–16. doi:10.1029/2006WR005233.

Lytle, D. A., and Merritt, D. M. (2004). HYDROLOGIC REGIMES AND RIPARIAN FORESTS: A STRUCTURED POPULATION MODEL FOR COTTONWOOD. Ecology 85, 2493–2503. doi:10.1890/04-0282.

Madsen, J. D. (2000). Advantages and Disadvantages of Aquatic Plant Management Techniques. ENGINEER RESEARCH AND DEVELOPMENT CENTER VICKSBURG MS ENVIRONMENTAL LAB Available at: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.513.3522&rep=rep1&type=pdf [Accessed July 1, 2016].

Magilligan, F. J., and Nislow, K. H. (2005). Changes in hydrologic regime by dams. Geomorphology 71, 61–78. doi:10.1016/j.geomorph.2004.08.017.

Mahoney, J. M., and Rood, S. B. (1998). Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands 18, 634–645.

Mainstone, C. P., and Parr, W. (2002). Phosphorus in rivers - Ecology and management. Sci. Total Environ. 282–283, 25–47. doi:10.1016/S0048-9697(01)00937-8.

Makkay, K., Pick, F. R., and Gillespie, L. (2008). Predicting diversity versus community composition of aquatic plants at the river scale. Aquat. Bot. 88, 338–346. doi:10.1016/j.aquabot.2007.12.011.

Merritt, D. M., Scott, M. L., Leroy Poff, N., Auble, G. T., and Lytle, D. A. (2010). Theory, methods and tools for determining environmental flows for riparian vegetation: Riparian vegetation-flow response guilds. Freshw. Biol. 55, 206–225. doi:10.1111/j.1365-2427.2009.02206.x.

Moher, D., Shamseer, L., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., et al. (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. Syst. Rev. 4, 1. doi:10.1186/2046-4053-4-1.

Narumalani, S., Jensen, J. R., Althausen, J. D., Burkhalter, S., and Mackey, H. E. (1997). Aquatic macrophyte modeling using GIS and logistic multiple regression. Photogramm. Eng. Remote Sensing 63, 41–49.

Nilsson, C., and Berggren, K. (2000). Alterations of riparian ecosystems caused by river regulation dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our. Bioscience 50, 783--792. doi:10.1641/0006-3568(2000)050[0783:AORECB]2.0.CO;2.

O'Hare, M. T. (2015). Aquatic vegetation - A primer for hydrodynamic specialists. J. Hydraul. Res. 53, 687–698. doi:10.1080/00221686.2015.1090493.

Olden, J. D., Jackson, D. A., and Peres-Neto, P. R. (2002). Predictive models of fish species distributions: a note on proper validation and chance predictions. Trans. Am. Fish. Soc. 131, 329–336. doi:10.1577/1548-8659(2002)131<0329:PMOFSD>2.0.CO;2.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. Bioscience 51, 933. doi:10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2.

Oorschot, M. van, Kleinhans, M., Geerling, G., and Middelkoop, H. (2016). Distinct patterns of interaction between vegetation and morphodynamics. Earth Surf. Process. Landforms 41, 791–808. doi:10.1002/esp.3864.

Paice, R. L., Chambers, J. M., and Robson, B. J. (2016). Native submerged macrophyte distribution in seasonally-flowing, south-western Australian streams in relation to stream condition. Aquat. Sci., 1–15. doi:10.1007/s00027-016-0488-x.

Pasgaard, M., and Strange, N. (2013). A quantitative analysis of the causes of the global climate change research distribution. Glob. Environ. Chang. 23, 1684–1693. doi:10.1016/j.gloenvcha.2013.08.013.

Pearlstine, L., McKellar, H., and Kitchens, W. (1985). Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. Ecol. Modell. 29, 283–302. doi:10.1016/0304-3800(85)90057-2.

Perona, P., Molnar, P., Crouzy, B., Perucca, E., Jiang, Z., McLelland, S., et al. (2012). Biomass selection by floods and related timescales: Part 1. Experimental observations. Adv. Water Resour. 39, 85–96. doi:10.1016/j.advwatres.2011.09.016.

Peterson, A. T., Papeş, M., and Soberón, J. (2015). Mechanistic and Correlative Models of Ecological Niches. Eur. J. Ecol. 1, 28–38. doi:10.1515/eje-2015-0014.

Petts, G. E., and Gurnell, A. M. (2005). Dams and geomorphology: Research progress and future directions. Geomorphology 71, 27–47. doi:10.1016/j.geomorph.2004.02.015.

Pickering, C., and Byrne, J. (2014). The benefits of publishing systematic quantitative literature reviews for PhD candidates and other early-career researchers. High. Educ. Res. Dev. 33, 534–548. doi:10.1080/07294360.2013.841651.

Poff, N. L., Allan, J. D., Bain, M. B., and Karr, J. R. (1997). Natural Flow Regime. Bioscience, 769–784. Available at: http://www.jstor.org/stable/1313099.

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., et al. (1988). Patch Dynamics in Lotic Systems: The Stream as a Mosaic. J. North Am. Benthol. Soc. 7, 503–524. doi:10.2307/1467303.

Rääpysjärvi, J., Hämäläinen, H., and Aroviita, J. (2016). Macrophytes in boreal streams: Characterizing and predicting native occurrence and abundance to assess human impact. Ecol. Indic. 64, 309–318. doi:10.1016/j.ecolind.2016.01.014.

Riis, T., and Biggs, B. J. F. (2003). Hydrologic and hydraulic control of macrophyte establishment and performance in streams. Limnol. Oceanogr. 48, 1488–1497. doi:10.4319/lo.2003.48.4.1488.

Riis, T., Suren, A. M., Clausen, B., and Sand-Jensen, K. (2008). Vegetation and flow regime in lowland streams. Freshw. Biol. 53, 1531–1543. doi:10.1111/j.1365-2427.2008.01987.x.

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., et al. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography (Cop.). 40, 913–929. doi:10.1111/ecog.02881.

Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E., and Lundquist, C. J. (2017). A systematic review of marine-based Species Distribution Models (SDMs) with recommendations for best practice. Front. Mar. Sci. 4, 1–11. doi:10.3389/fmars.2017.00421.

Salager-Meyer, F. (2008). Scientific publishing in developing countries: Challenges for the future. J. English Acad. Purp. 7, 121–132. doi:10.1016/j.jeap.2008.03.009.

Schaepman, M. E., Wamelink, G. W. W., van Dobben, H. F., Gloor, M., Schaepman-Strub, G., Kooistra, L., et al. (2007). River Floodplain Vegetation Scenario Development Using Imaging Spectroscopy Derived Products as Input Variables in a Dynamic Vegetation Model. Photogramm. Eng. Remote Sens. 73, 1179–1188. doi:10.14358/PERS.73.10.1179.

Schmolke, A., Thorbek, P., DeAngelis, D. L., and Grimm, V. (2010). Ecological models supporting environmental decision making: A strategy for the future. Trends Ecol. Evol. 25, 479–486. doi:10.1016/j.tree.2010.05.001.

Solari, L., Van Oorschot, M., Belletti, B., Hendriks, D., Rinaldi, M., and Vargas-Luna, A. (2016). Advances on Modelling Riparian Vegetation-Hydromorphology Interactions. River Res. Appl. 32, 164–178. doi:10.1002/rra.2910.

Son, D., Cho, H., and Lee, E. J. (2018). Determining factors for the occurrence and richness of submerged macrophytes in major Korean rivers. Aquat. Bot. 150, 82–88. doi:10.1016/j.aquabot.2018.07.003.

Sousa, W. T. Z., Thomaz, S. M., Murphy, K. J., Silveira, M. J., and Mormul, R. P. (2009). Environmental predictors of the occurrence of exotic Hydrilla verticillata (L.f.) Royle and native Egeria najas Planch. in a sub-tropical river floodplain: the Upper River Paraná, Brazil. Hydrobiologia 632, 65–78. doi:10.1007/s10750-009-9828-3.

Spencer, D. F., and Carruthers, R. I. (2013). Predicting Eurasian watermilfoil's (Myriophyllum spicatum) distribution and its likely response to biological control in a spring-fed river. J. Aquat. Plant Manag. 51, 7–14.

Tabacchi, E., Correll, D. L., Hauer, R., Pinay, G., Planty-Tabacchi, A. M., and Wissmar, R. C. (1998). Development, maintenance and role of riparian vegetation in the river landscape. Freshw. Biol. 40, 497–516. doi:10.1046/j.1365-2427.1998.00381.x.

Thomaz, S. M., and Cunha, E. R. da (2010). The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnol. Bras. 22, 218–236. doi:10.4322/actalb.02202011.

Tickner, D. P., Angold, P. G., Gurnell, A. M., and Mountford, J. O. (2001). Riparian plant invasions: Hydrogeomorphological control and ecological impacts. Prog. Phys. Geogr. 25, 22–52. doi:10.1191/030913301673178792.

Tinoco, A. I., Furman, B. T., Darnell, K. M., and Peterson, B. J. (2017). Submerged aquatic vegetation, topography and flow characteristics in the upper, tidal Hudson River: Progress toward a predictive habitat model. Aquat. Bot. 142, 53–60. doi:10.1016/j.aquabot.2017.06.006.

Toner, M., and Keddy, P. (1997). River hydrology and riparian wetlands: A predictive model for ecological assembly. Ecol. Appl. 7, 236–246. doi:10.1890/1051-0761(1997)007[0236:RHARWA]2.0.CO;2.

Van Den Berg, M. S., Joosse, W., and Coops, H. (2003). A statistical model predicting the occurrence and dynamics of submerged macrophytes in shallow lakes in the Netherlands. Hydrobiologia 506–509, 611–623. doi:10.1023/B:HYDR.0000008610.97044.39.

van Ek, R., Witte, J.-P. M., Runhaar, H., and Klijn, F. (2000). Ecological effects of water management in the Netherlands: the model DEMNAT. Ecol. Eng. 16, 127–141. doi:10.1016/S0925-8574(00)00097-5.

Van Noordwijk, M., Lawson, G., Hairiah, K., and Wilson, J. (2015). Root distribution of trees and crops: competition and/or complementarity. Tree–Crop Interact. Agrofor. a Chang. Clim. CABI, Wallingford, UK, 221–257.

Vis, C., Hudon, C., and Carignan, R. (2003). An evaluation of approaches used to determine the distribution and biomass of emergent and submerged aquatic macrophytes over large spatial scales. Aquat. Bot. 77, 187–201. doi:10.1016/S0304-3770(03)00105-0.

Woodward, G., and Hildrew, A. G. (2002). Food web structure in riverine landscapes. Freshw. Biol. 47, 777–798. doi:10.1046/j.1365-2427.2002.00908.x.

Ye, F., Chen, Q., Blanckaert, K., and Ma, J. (2013). Riparian vegetation dynamics: Insight provided by a process-based model, a statistical model and field data. Ecohydrology 6, 567–585. doi:10.1002/eco.1348.

You, X., Liu, J., and Zhang, L. (2015). Ecological modeling of riparian vegetation under disturbances: A review. Ecol. Modell. 318, 293–300. doi:10.1016/j.ecolmodel.2015.07.002.

Zefferman, E. P., and Harris, D. J. (2016). Predicting drivers of nuisance macrophyte cover in a regulated California stream using boosted regression tree models. J. Aquat. Plant Manag. 54, 78–86.

Zurell, D., Jeltsch, F., Dormann, C. F., and Schröder, B. (2009). Static species distribution models in dynamically changing systems: How good can predictions really be? Ecography (Cop.). 32, 733–744. doi:10.1111/j.1600-0587.2009.05810.x.

3 FLOW MANAGEMENT TO CONTROL EXCESSIVE GROWTH OF MACROPHYTES – AN ASSESSMENT BASED ON HABITAT SUITABILITY MODELING

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3.1 Abstract

Mediterranean rivers in intensive agricultural watersheds usually display outgrowths of macrophytes – notably alien species – due to a combination of high concentrations of nutrients in the water runoff and low flows resulting from water abstraction for irrigation. Standard mechanical and chemical control is used to mitigate the problems associated with excessive growth of plant biomass: mainly less drainage capacity and higher flood risk. However, such control measures are cost and labor-intensive and do not present long-term efficiency.

Although the high sensitivity of aquatic vegetation to instream hydraulic conditions is well known, management approaches based on flow management remain relatively unexplored. The aim of our study was therefore to apply physical habitat simulation techniques promoted by the Instream Flow Incremental Method (IFIM) to aquatic macrophytes – the first time it has been applied in this context – in order to model shifts in habitat suitability under different flow scenarios in the Sorraia river in central Portugal. We used this approach to test whether the risk of invasion and channel encroachment by nuisance species can be controlled by setting minimum annual flows.

We used 960 randomly distributed survey points to analyze the habitat suitability of the physical parameters ‘flow velocity’, ‘water depth’ and ‘substrate size’ for the most important aquatic species, including the invasive Brazilian milfoil *Myriophyllum aquaticum, Sparganium erectum* and *Potamogeton crispus*. We chose the lowest discharge period of the year in order to assess the hydraulic conditions while disturbances were at a low-point, thus allowing aquatic vegetation establishment and subsistence. We then used the two-dimensional hydraulic River2D software to model the potential habitat availability for different flow conditions based on the site-specific habitat suitability index for each physical parameter and species.

Our results show that the growth and distribution of macrophytes in the hydrologically stable vegetation period is primarily a function of the local physical instream condition. Using site-specific preference curves and a two-dimensional hydraulic model, it was possible to determine minimum annual flows that might prevent the excessive growth and channel encroachment caused by *Myriophyllum aquaticum*.

Keywords: aquatic macrophytes, habitat suitability modeling, flow regulation, invasive species, Myriophyllum aquaticum, IFIM

3.2 Introduction

Aquatic macrophytes play an important role in riverine ecosystems, providing habitats for many organisms and affecting the hydraulic and chemical instream condition (Carpenter and Lodge, 1986). Their distribution and abundance are primarily determined by the hydrologic regime (frequency, duration and intensity of flood events) (Riis and Biggs, 2003; Franklin et al., 2008), which controls biomass loss and gain processes. Whereas loss processes are caused by increased drag forces during high flood events that cause stem breakage and uprooting of plants, biomass gain processes happen while disturbances are absent during medium to low flow conditions (Riis et al., 2008). In these stable interflood periods, macrophyte growth is controlled by several physical and chemical factors, including flow velocity and depth (Chambers et al., 1991; Riis and Biggs, 2003), light availability (Carr et al., 1997; Köhler et al., 2010), water temperature (Barko et al., 1986; Carr et al., 1997), and riverbed grain size (Baattrup-Pedersen and Riis, 1999), as well as the nutrient content of the riverbed and water (Barko et al., 1986; Demars and Edwards, 2009). Anthropogenic disturbances, such as high nutrient concentrations from water runoff (Jones et al., 2002; Mainstone and Parr, 2002), low suspended sediment concentrations and the resulting increase in light availability from river damming (Madsen et al., 2001; Köhler et al., 2010) and stabilization of the flow regime (less floods) (Riis and Biggs, 2003; Franklin et al., 2008) can alter the ecological equilibrium of the system and have been shown to stimulate excessive growth of aquatic vegetation, notably invasive alien species (Bunn and Arthington, 2002). This is known to cause various forms of ecological and economic damage (Brundu, 2014), including changes in species composition and richness (Bunn and Arthington, 2002; O'Hare et al., 2006), increased flood risk through higher flow resistance (Vereecken et al., 2006; Nikora et al., 2008), and interferences with human water uses such as water abstraction, hydropower, recreation and river navigation (Halstead et al., 2003; Gómez et al., 2013). Management of aquatic macrophytes by mechanical (cutting) or chemical (herbicides) means is therefore common practice in many rivers worldwide (Madsen, 2000; Hussner et al., 2017).

Especially in regulated Mediterranean rivers flowing through intensive agricultural watersheds and presenting prolonged spells of low flows the outgrowth of aquatic vegetation, and notably alien species, is a common phenomenon (Ferreira and Moreira, 1999; Aguiar and Ferreira, 2013). Despite their high costs, mechanical control measures are widely applied in Portugal (Moreira et al., 1999).

Although the growth and distribution of aquatic macrophytes in unshaded streams are mainly influenced by local hydraulic conditions (depth/velocity/sediments) (Chambers et al., 1991; Riis and Biggs, 2003), whose impact overshadows that of hydrochemistry (Steffen et al., 2014), little attention has thus far been paid to the possibility that channel encroachment and invasion can be controlled by establishing minimum annual flows. One common way of exploring the effectiveness of such ecosystem-regulation measures is ecological modeling because model-based testing is faster and requires less financial inputs than actual physical experiments (Perona et al., 2009; Schmolke et al., 2010). Modeling species distribution or habitat suitability as functions of environmental factors is frequently used to provide spatial decision support for environmental management, weed or pest species risk assessments and studies of climate-change impacts (Franklin, 2013). In the case of river ecosystems, the instream flow incremental method (IFIM) (Bovee, 1982; Raleigh et al., 1986) is probably still the most widely used and accepted methodology for predicting the response of aquatic biota to the instream physical condition (Jowett et al., 2008; Conallin et al., 2010). However, its concepts have never been directly applied to the management of aquatic macrophytes.

Against this background, the main aim of this study was, for the first time, to apply and validate the hydraulic habitat modeling techniques promoted by the IFIM for the assessment of annual minimum flows with the ability to reduce the risk of channel encroachment and invasion by the alien *Myriophyllum aquaticum* in a heavily regulated Mediterranean river. Our hypothesis was that summer low flows further intensified by water abstraction for irrigation create physical instream conditions that favor the excessive growth of *Myriophyllum aquaticum* over the autochthonous *Sparganium erectum* and *Potamogeton crispus*, and that this situation can be mitigated by establishing minimum flows above a certain threshold.

3.3 Methodology

3.3.1 Study Area

The study area is located along the Sorraia river in central Portugal (Figure 9). The river basin has an accumulated area of 7719 km² and a semi-arid Mediterranean climate in which most of the annual rainfall (600–800 mm) occurs between October and May and the mean annual temperature is 16-19 °C. The fieldwork was carried out along a naturally braided, unconfined segment of the river. The riparian corridor from the edge of the active channel to the adjacent agricultural areas consists mostly of willow shrubs, and willows (*Salix alba*) in higher areas, and extends an average of 60 m either side of the river. The active channel has an average width of 15 m and is mostly unshaded. The segment's substrate is dominated by sands, gravels and cobbles. Surrounding land is given over to intensive rice, maize and tomato cultivation. We chose a calibration reach of approximately 1000 m in length for the model-building, and a model reach with a length of 320 m directly downstream for testing and application. Both reaches contain all the different mesohabitats (pool/run/riffle) found in the segment.

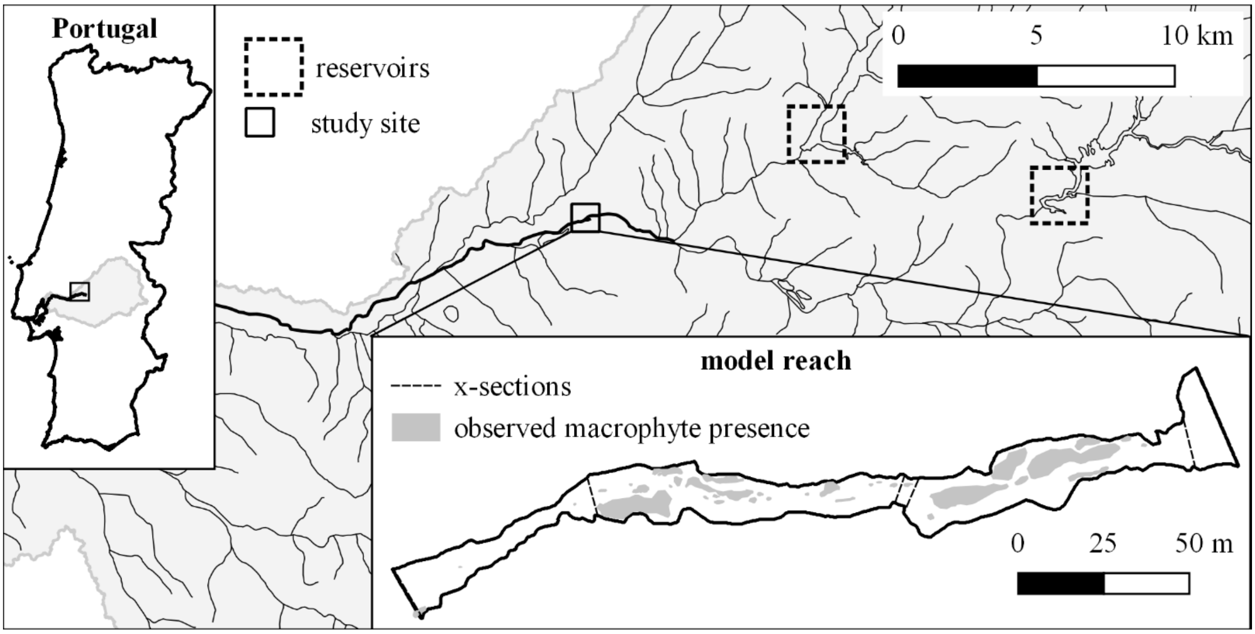

Figure 9: Location of the study site in Portugal and the Sorraia basin (rectangle), the position of the two largest reservoirs (dotted rectangles) and the wetted area of the model reach at Q = 0.3 m^3/s, the location of the x-sections used for the hydraulic model calibration (including boundaries), and the observed macrophyte presence used to validate the habitat suitability model

The Sorraia's hydrological regime presents a high intra- and inter-annual discharge variability, which is characteristic of Mediterranean watersheds (Gasith and Resh, 1999). The mean annual discharge is 20.14 m^3/s (available data for 1933-1980, "Ponte Coruche" Gauging station). The heaviest winter floods can attain 887 m^3/s, while during the summer months (June-September) the mean discharge is 3.2 m^3/s and low flow spells are common (Figure 10).

The flow regime is heavily regulated by a system of reservoirs, weirs and canals that was implemented between 1933 and 1958. Water abstraction for agricultural irrigation is managed by a local farmers' association, which mechanically cleans the river channel of aquatic macrophytes and riparian vegetation every few years to reduce flood risk.

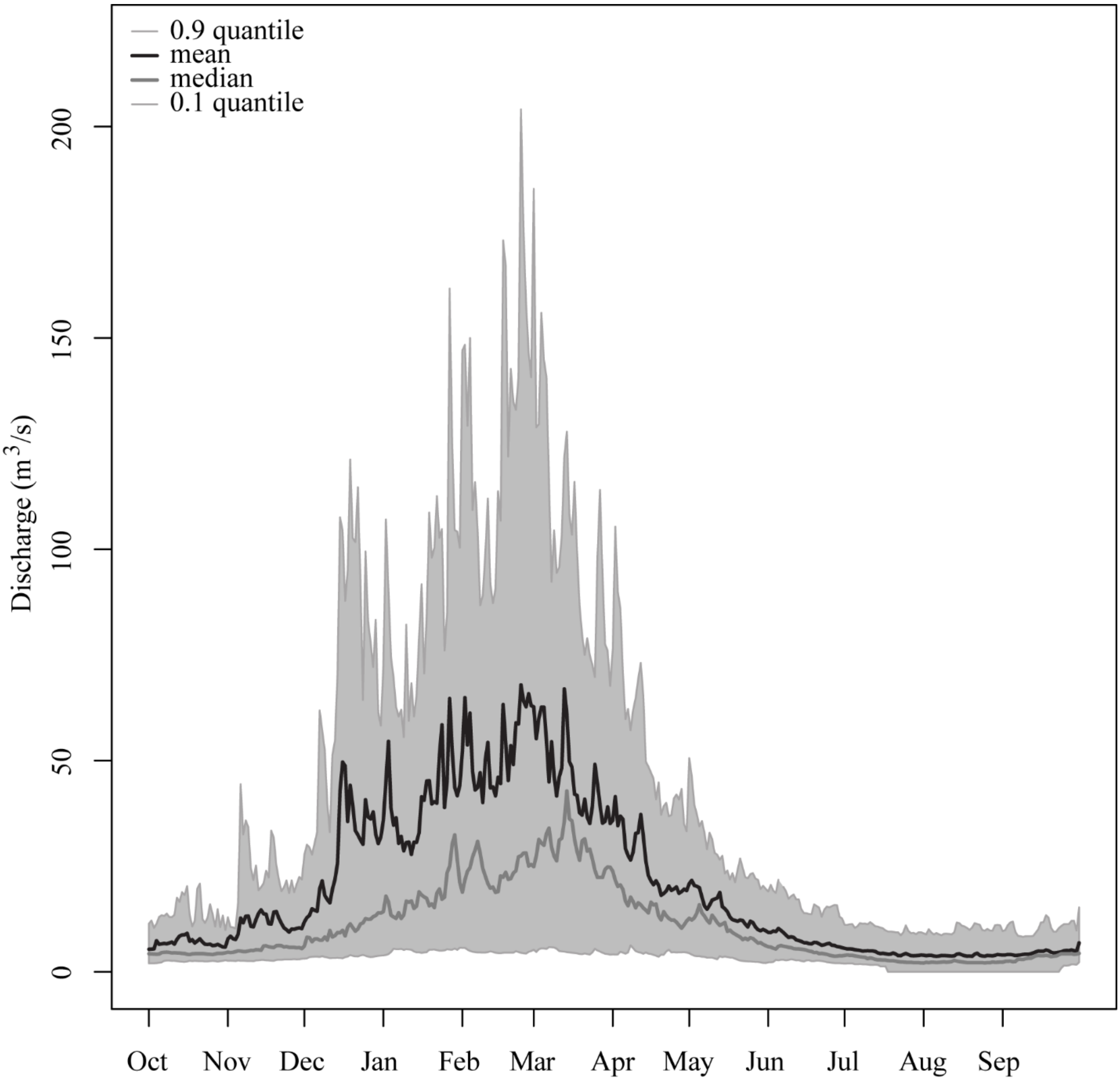

Figure 10: Summary of the flow regime of the Sorraia river (available data for 1933-1980 from the “Ponte Coruche” Gauging station): The area between the upper (0.9) and lower (0.1) quantiles is shaded grey; the black line represents the mean daily discharge; the grey line represents the median daily discharge

3.3.2 Aquatic vegetation

The main aquatic macrophyte species occurring in the study area are *Myriophyllum aquaticum*, *Sparganium erectum* and *Potamogeton crispus*. Other species that presented less prevalence and were therefore not considered were *Ceratophyllum demersum* and *Typha domingensis.* Based on their growth form, *Myriophyllum aquaticum* and *Sparganium erectum* are classified as sediment-rooted plants with floating or emergent shoots/leaves, whereas *Potamogeton crispus* is a sediment-rooted submerged plant (Den Hartog and Van Der Velde, 1988). Following the definition of Pyšek et al. (2013) *Myriophyllum aquaticum* is considered an invasive species in Portugal. It was first reported in 1936 (Aguiar and Ferreira, 2013), but massive spreading was only observed in the 1970s (Moreira et al., 1999). *Myriophyllum aquaticum* is displacing native aquatic species, including *Potamogeton crispus* and *Ceratophyllum demersum*, in many parts of the River Tagus (Ferreira and Moreira, 1995).

3.3.3 IFIM overview

The instream flow incremental methodology (Bovee, 1982; Raleigh et al., 1986) is a framework which the U. S. Fish and Wildlife Services developed in the late 1970s to determine appropriate minimum annual flows by considering the effects of flow changes on instream habitat suitability of aquatic biota. It is probably still the most widely used and accepted methodology for predicting the response of aquatic biota to the instream physical condition (Jowett et al., 2008; Conallin et al., 2010). Its main feature is a hydraulic habitat suitability model that can be separated into a hydraulic component and a habitat component. The hydraulic model predicts water velocity, depth and other hydraulic variables. The habitat model is based on local habitat suitability curves (HSC) that describe the optimum range of a physical parameter affecting the species and are built on expert knowledge or field analyses of local species occurrence and habitat availability. Integrating the two components makes it possible to calculate a composite suitability index (CSI) that combines the suitability information for each physical parameter at a given flow. The weighted usable area (WUA) for the target species is quantified by multiplying the composite suitability index by its area of influence. In order to assess an appropriate minimum annual flow, the hydraulic habitat suitability model is applied to a range of flows to produce a WUA-vs-discharge graph.

3.3.4 Hydraulic Habitat Suitability Modelling

In order to calibrate (train) the habitat suitability model, a total of 961 sample points were distributed systematically (2m x 2m), with a randomly chosen starting point along each mesohabitat (pool, run, riffle) found in the calibration reach. The mesohabitats were visually delimited in the field.

The occurrence of the main macrophyte species and physical habitat characteristics – flow velocity, water depth and grain size of the bed material – were analyzed at each sample point. The fieldwork was done in August 2016 and July 2017, during measured discharges of around 0.3 m^3/s. We chose the lowest discharge period of the year in order to assess the hydraulic conditions during the period of least disturbance, which allows aquatic vegetation establishment and subsistence. Locations shaded by riparian vegetation (less than 5% of the analyzed reach) were excluded, since in this situation aquatic plant growth is mainly constrained by insufficient light (Carr et al., 1997). Depths were measured with a simple meter ruler and classified in intervals of 20 cm. Flow velocities were measured with a water flow probe (model FP101, Global Water Instrumentation, USA) positioned in the flow direction at 60 % of the flow depth and using 0.05 m/s intervals. The bed grain size was assessed visually and classified according to the Wentworth scale (sand: 0.62 - 2 mm; gravel: 2 - 64 mm; cobble: 64 - 256 mm). The habitat preferences for *Myriophyllum aquaticum*, *Sparganium erectum* and *Potamogeton crispus* were then calculated by dividing habitat-utilization (amount of species occurrences in each class of the physical parameters) by habitat-availability (total amount of each class of the physical parameters). The final preference values were normalized, from a minimum value of 0 for unsuitable to 1.0 for optimal habitats (the class of the physical parameter with the highest amount of species occurrences), and expressed as a habitat suitability curve (HSC) for each physical parameter.

In order to apply and test the hydraulic habitat suitability model, we selected a 320 m-long reach directly downstream from the calibration reach. We chose a two-dimensional approach for the hydraulic simulation: the River2D model (Steffler and Blackburn, 2002). Two-dimensional hydraulic models predict depth and velocity laterally and longitudinally along the whole length of the river channel. They are therefore better able to simulate the complex flow patterns found in braided rivers than the more conventional (with regard to the IFIM) one-dimensional models that only predict depth and velocity across channel transects (Benjankar et al., 2015). The topography of the riverbed of the model reach, which is the main input into the hydraulic model, was measured in July 2016 with a Leica TCR703 Total Station (angle accuracy 3”) along 970 points. The initial bed roughness values were estimated based on substrate size and vegetation distribution. To determine the boundary condition and calibrate the model, water depth and velocity were assessed along 6 transects including the down- and upstream cross-section, with measurements taken every 20 cm along the cross-section. The hydraulic model was calibrated by adjusting bed roughness until simulated water surface elevations matched measured water surface elevations.

The model was then used to simulate the physical instream conditions for a series of potential annual minimum flows of between 0.3 and 10 m^3/s, representing a common flow range during the vegetation period. The weighted usable area (WUA) concept was used to evaluate the shift in habitat suitability for each discharge (Bovee, 1982). The WUA computation is based on the habitat suitability evaluated at every node of the topographic mesh and the "tributary area" of that node. We also calculated the Hydraulic Habit Suitability (HHS) for each discharge by dividing the WUA by the inundated area. The HHS can be understood as the percentage of the WUA from the inundated area at a given discharge. A value of 1 would mean that the whole of the wetted area classifies as usable area for a certain species or species group.

We used two different methods to calculate the habitat suitability. The classical, deterministic approach of the IFIM calculates a Composite Suitability Index (CSI) as the geometric mean of the separate suitability indices for depth, velocity, and substrate size. It is directly integrated into the River2D Model on the basis of the HSC for each species.

$$CSI = \sqrt[3]{(VSI \times DSI \times SSI)}$$

VSI - Velocity Suitability Index

DSI – Depth Suitability Index

SSI – Substrate Suitability Index

In addition to the deterministic approach, we computed the habitat suitability for each species based on the random forest algorithm (RF) for classification (Breiman, 2001). We used the R package "randomForest" (Liaw and Wiener, 2002) to grow 1000 trees based on bootstrap samples of the same training data as that used to build the HSC, and incorporated 50% class weights into the classifier to account for the low prevalence of *Potamogeton crispus* and *Sparganium erectum*.

3.3.5 Model Validation

We mapped the true presence and absence of the main macrophyte species (*Myriophyllum aquaticum*, *Sparganium erectum* and *Potamogeton crispus*) in the model reach with a Global Positioning System unit (Ashtech, model Mobile Mapper 100; accuracy < 50 cm) during the same period (July/August) and with the same discharge (0.3 m^3/s) as those when the data for the model calibration was collected. We then modeled the macrophyte distribution using the deterministic and the random forest approach based on the hydraulic simulation for the same discharge, and tested the agreement between observed and predicted distribution by assessing the area under the receiver operating characteristic curve (AUC) (Fielding and Bell, 1997). The AUC of a model is equivalent to the probability that the model will rank a randomly chosen species-presence site higher than a randomly chosen absence site. In addition, we transformed the predicted occurrence probabilities of both models to a binary presence/absence format for each species using the threshold of occurrence that maximizes the sum of sensitivity and specificity (Cantor et al., 1999; Liu et al., 2005). In order to assess the accuracy of the binary classification, we used the "True Skill Statistic" (TSS; sensitivity + specificity – 1), because it accounts for the effect of the species prevalence (Allouche et al., 2006). All accuracy measurements were carried out using the R package "SDMtools" (VanDerWal et al., 2014).

In order to investigate whether our models accounted for all the factors causing the species' distributional pattern, we checked the observed species occurrence in the model reach for spatial autocorrelation using the Ripley's K function, and tested the error between observed and predicted species occurrence for clustering with the Moran's I index. The spatial analyses were done with the spatial statistics toolbox from ArcGIS for desktop (version 10.4.1).

3.4 Results

3.4.1 Habitat Suitability Curves

The habitat sampling resulted in 224 *Myriophyllum aquaticum*, 135 *Potamogeton crispus* and 85 *Sparganium erectum* presences in a total of 961 habitat samples.

Myriophyllum aquaticum displayed a substantial liking for low flow conditions, only having colonized areas with relatively slow velocities and low depth. It was already nearly absent at velocities over 0.1 m/s. The most suitable depths were 0-20 cm. In addition, it was found almost exclusively on sandy substrate. On the contrary, *Potamogeton crispus* seemed to prefer higher-flow areas. Its greatest presence occurred in medium velocities of 0.08 - 0.2 m/s and it clearly favored depths of more than 80 cm. Its preferred substrate was gravel. *Sparganium erectum* displayed a preference profile similar to that of *Myriophyllum aquaticum*, but was more tolerant of greater depth. The results show a distinct preference profile of the exotic *Myriophyllum aquaticum* with regard to flow velocity and water depth (Figure 11).

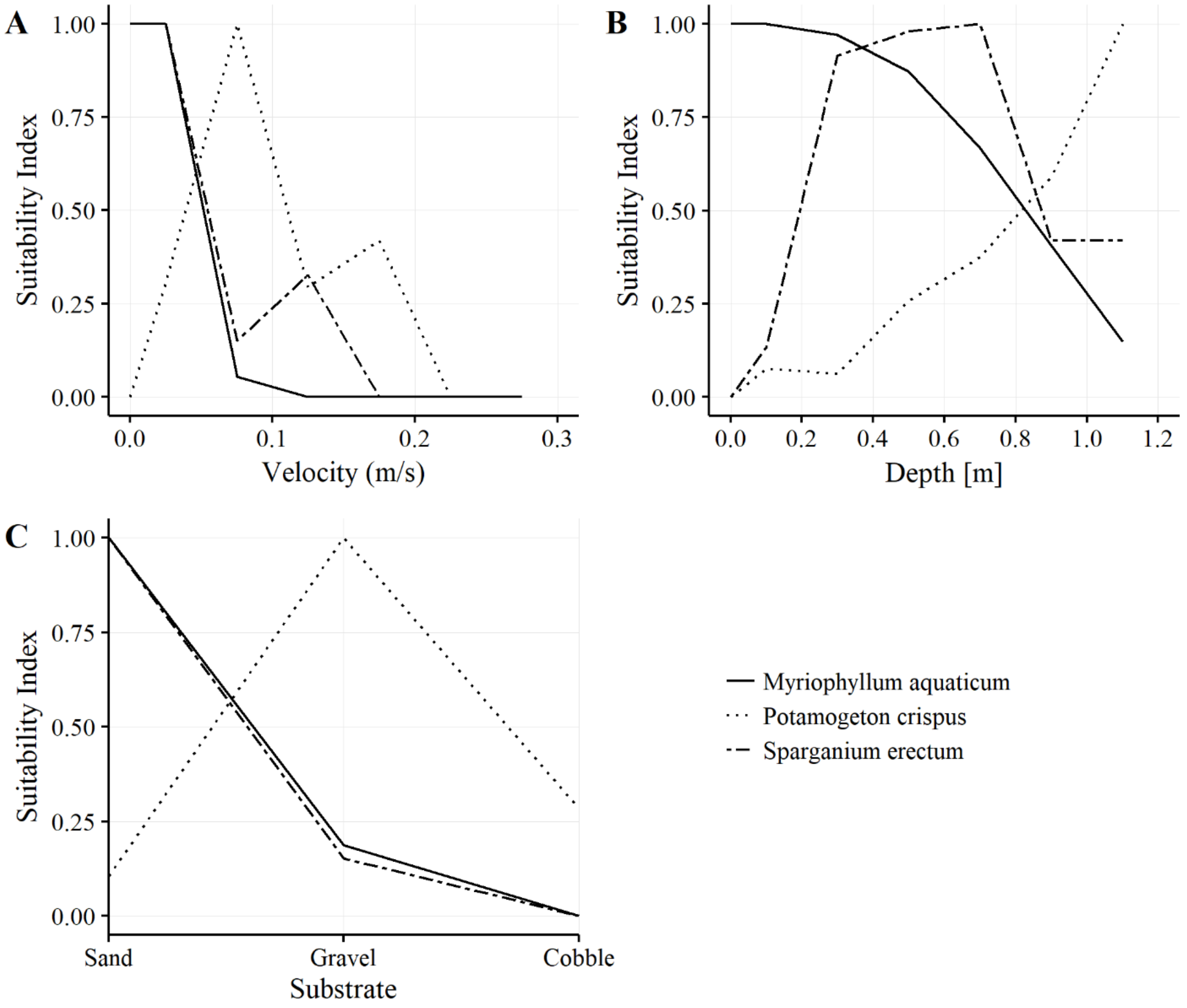

Figure 11: Suitability Index (SI) with regard to flow velocity (A), water depth (B), and substrate size of the bed material (C) for *Myriophyllum aquaticum*, *Potamogeton crispus and Sparganium erectum;* values of 1 signify optimal and values of 0 signify no suitability.

3.4.2 Model validation

In overall terms, the hydraulic habitat model based on the deterministic approach displayed a good discriminatory ability. In the case of *Myriophyllum aquaticum*, accuracy was even in the excellent range (AUC = 0.9), while for *Potamogeton crispus* it was good (AUC = 0.87), and for *Sparganium erectum* fair (AUC = 0.79). The performance of the binary classification differed more drastically between the species. Considering a threshold of occurrence for *Myriophyllum aquaticum* of 0.24, the TSS score of the model was 0.66. It correctly predicted 86% of the actual presences (sensitivity) and 80% of the actual absences (specificity). The occurrence threshold for *Potamogeton* was set to 0.24. The TSS score was 0.62. Its occurrence was correctly predicted in 88% of cases, and its absence in 70%. The model's worst performance was for *Sparganium erectum*, with an occurrence threshold of 0.08 (TSS = 0.44; Sensitivity = 0.7; Specificity = 0.66).

The random forest model did not perform as well as the deterministic approach. On the contrary, only the prediction of *Myriophyllum aquaticum* achieved a similar accuracy (AUC = 0.85), whereas the predictions for *Potamogeton crispus* (AUC = 0.7) and *Sparganium erectum* (AUC = 0.65) were less accurate. This was also visible in the binary prediction. Considering a threshold of occurrence of 0.6 for *Myriophyllum aquaticum,* the model's TSS score was 0.66 (sensitivity = 0.8; specificity = 0.86). The prediction of *Potamogeton* based on a threshold of 0.5 returned a TSS score of 0.38 (sensitivity = 0.66; specificity = 0.72). Once again, the model performed worst for *Sparganium erectum* (threshold = 0.2; TSS = 0.28; sensitivity = 0.66; specificity = 0.62).

The species occurrence as well as the errors between the observed and predicted distributions presented a similar degree of positive spatial autocorrelation (clustered pattern), indicating that although our models have a medium to high degree of accuracy, they do not account for all the factors explaining species distribution.

3.4.3 Weighted Usable Area and Hydraulic Habitat Suitability

We only used the deterministic modeling approach to analyze the shifts in habitat suitability for incremental flows because of its better predictive performance.

The preference of *Myriophyllum aquaticum* for low flow conditions is also reflected in the development of the WUA. From 1167 m^2 at $Q = 0.3\ m^3/s$, it rapidly increases until it reaches its maximum of 3085 m^2 at $Q = 1.4\ m^3/s$. The WUA drops steadily after that, although the inundated and therefore potentially invadable area continues to increase with rising flows. The WUA decreases more slowly from Q = 5 m^3/s to Q = 8 m^3/s, after which it remains nearly constant. At Q = 0.3 m^3/s *Potamogeton crispus* has a WUA of 1017 m^2, slightly lower than that of *Myriophyllum aquaticum* and *Sparganium erectum*. However, this then sharply increases, so that at Q = 3 m^3/s the *Potamogeton crispus* WUA of 8004 m^2 is already 3 times higher than that of *Myriophyllum aquaticum*. After that, the upward trend continues more slowly, but steadily. At Q = 10 m^3/s, the *Potamogeton crispus* WUA of 10569 m^2 is over 10 times that of the invaders. The development of the WUA of *Sparganium erectum* initially appears to be similar to that of *Myriophyllum aquaticum*. However, it continues to gain area until Q = 3.5 m^3/s, after which the WUA stays relatively constant at around 3900 m^2, whereas the *Myriophyllum aquaticum* WUA experiences a steady decline over the same range (Fig. 04 – A).

In the case of *Myriophyllum aquaticum*, the HHS trends continuously downwards as discharge increases. Whereas 36% of the wetted area is potentially suitable at Q = 0.3 m^3/s, only about 10% remains suitable at Q = 4 m^3/s. *Potamogeton crispus* experiences an increase in HHS with rising flows. The HHS only decreases slightly at around Q = 1 m^3/s, due to a large increase in wetted area. From Q = 3.5 m^3/s onwards, the rate of change in HHS decreases. *Sparganium erectum* also experiences a decline in HHS, sharply at first, to levels below even those of *Myriophyllum aquaticum*, but remains nearly constant from Q = 2.5 m^3/s onwards (Fig. 04 – B).

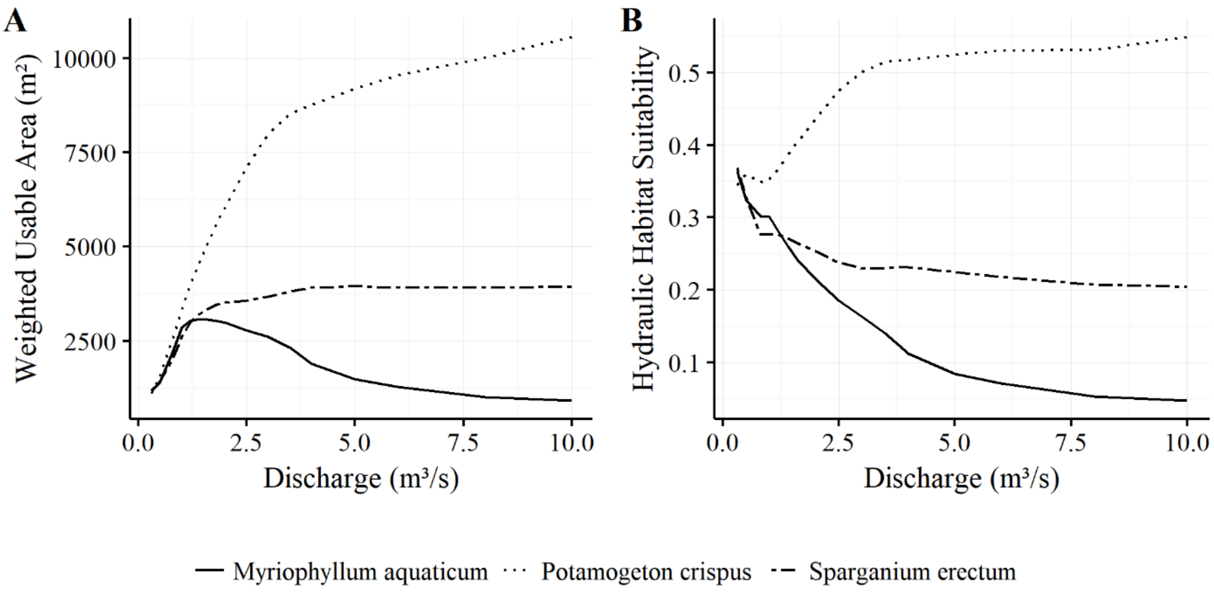

Figure 12: Weighted Usable Area (A) and Hydraulic Habitat Suitability (B) of the main species found in the study area as a function of discharge.

3.5 Discussion

In this study we wanted to explore setting minimum annual flows as an alternative management approach for controlling excessive growth of macrophytes and invasion by *Myriophyllum aquaticum* during the vegetation period in the Sorraia river. Following IFIM principles, we built a hydraulic habitat suitability model for *Myriophyllum aquaticum*, *Sparganium erectum* and *Potamogeton crispus*, applied it to a range of discharges, and analyzed the changes in WUA and HHS. Our hypothesis was that low summer flows intensified by water abstraction for irrigation create physical instream conditions that stimulate excessive growth of *Myriophyllum aquaticum*, and that this situation can be mitigated by establishing minimum flows above a certain threshold.

The modelling results support our hypothesis that the growth and distribution of macrophytes in interflood periods is primarily a function of the local physical instream condition, which is especially favorable to an invasion of *Myriophyllum aquaticum* during the low flow range. Habitat suitable for *Myriophyllum aquaticum* already declines above flows of 1.4 m³/s, while the autochthonous species, and especially *Potamogeton crispus,* continue to gain ground. It would therefore seem possible to reduce the risk of invasion and favor a more natural species composition by setting annual minimum flows. The combination of the artificial approximation of the habitat availability for both the exotic and the autochthonous species caused by stable periods of flows under 1.4 m^3/s and the greater competitive ability of *Myriophyllum aquaticum* may be the reason for the latter's successful expansion. Given that the mean annual flow during the vegetation period is 3.2 m^3/s, it may well be that water managers can establish minimum annual flows above the 1.4 m^3/s threshold and thereby avert this situation. This is an important result that can improve river restoration projects by preventing the degradation of natural aquatic vegetation communities.

However, we also observed that for the low flow range (0.3-1.4 m^3/s), the WUA actually increases for *Myriophyllum aquaticum* and that the rate of change in habitat suitability for all species is lower with high flows than with low flows. The explanation for this is that the suitable areas are concentrated in shallow waters along the banks of the stream, and these shallow areas initially increase when the river enters the floodplain and then remain relatively constant in size. In the case of *Myriophyllum aquaticum*, this means that the WUA remains relatively constant above a discharge of 7 m^3/s. Setting minimum annual flows will therefore not completely prevent an invasion; but it can contribute to an environmental flow regime that privileges autochthonous aquatic species and strengthens their competitive performance.

One major criticism of the IFIM habitat simulation to keep in mind when interpreting the results is the usage of the term Weighted Usable Area (Mathur et al., 1985), because it suggests a spatial extension of usable habitat when in fact it only actually describes the overall probability of use. So when we assess the effects of flow changes on aquatic biota, it is the shape of the WUA response curve that is more important than the magnitude (Jowett et al., 2008).

In addition, as with all modeling approaches, there are a number of different uncertainties that should be considered when interpreting the results.

3.5.1 Environmental factors

Our study is based on the assumption that in hydrologically stable periods, physical habitat characteristics are the main limiting factor for aquatic species in streams. Indeed, several studies argue that flow velocity is the main environmental factor controlling the abundance and distribution of aquatic macrophytes (Chambers et al., 1991; Baattrup-Pedersen and Riis, 1999; Madsen et al., 2001; Janauer et al., 2010). Most studies relate the limiting effect of higher flow velocities on plant growth to increased drag forces on the plants and their anchoring ground, causing uprooting, or less frequently, stem breakage (Chambers et al., 1991; Riis and Biggs, 2003). However, a more recent study (Pollen-Bankhead et al., 2011) indicates that the preference of macrophytes for low velocities is less related to the drag forces on the plants and more to the conditions controlling erosion and deposition of fine substrate materials. The effect of substrate size has mainly been studied with regard to the distribution patterns of macrophytes, and not in terms of changes in biomass (Baattrup-Pedersen and Riis, 1999; Riis and Biggs, 2001; O'Hare et al., 2006). The findings indicate a niche separation between macrophytes based on different substrate size preferences. Apparently, submerged species favor coarser substrates (gravel and boulder), whereas species that grow both submerged and emergent, and species that only grow emergent, were associated with finer substrates (sand) typical of low flow conditions. This is coherent with our results. The influence of flow depth has been related to light availability, which decreases with greater depth (Koch, 2001). In situations of high turbidity or direct shading, for example through overhanging vegetation, light availability can also become the main limiting factor, which is why we excluded sample sites with these characteristics (Köhler et al., 2010). Temperature is also known to influence the growth rate of aquatic plants (Koch, 2001). It can, however, be assumed that temperature alterations in the analyzed flow range are marginal and are indirectly covered by the effects of velocity and depth (Gu et al., 1998). Besides the physical factors, geochemical properties of the stream and especially nutrient availability are known to have an influence on aquatic biota (Koch, 2001). Unnatural high concentrations of phosphorus, as often occur in agricultural watersheds, can stimulate excessive macrophyte growth (Mainstone and Parr, 2002). However, these factors are still most probably overshadowed by the hydraulic conditions (Barendregt and Bio, 2003; Steffen et al., 2014), as is also indicated by the high accuracy of our model.

3.5.2 Data collection / Model calibration

Different forms of data analysis for generating the HSC for each environmental factor are distinguished for the IFIM (Bovee, 1986): a) expert knowledge; b) analyses of actual habitat conditions used by the species (or presence-only data); and c) in-situ species occurrence and habitat availability data (or presence/absence data). We based our model calibration solely on actual presence/absence data (c). It is the most highly recommended of the three methods (Jowett et al., 2008), and the only one that permits an estimation of the true probability of observing a species at a site (Guillera-Arroita et al., 2015). We kept geographical sampling bias to a minimum by selecting a calibration (training) reach and a model reach from the same river segment, and by applying a stratified, systematic sampling design with a random starting point. The detection error, which is crucial to the performance of many habitat suitability models (Lahoz-Monfort et al., 2014), can be considered negligible because of the sampling design, the small number of different species and their sessility.

Model calibration errors can also affect the two-dimensional hydraulic modeling, which can be compromised due to the collection of insufficient or erroneous bed topography data, insufficiently detailed substrate distribution mapping, erroneous model calibration, or failure to include effects of the bed topography upstream of the study site in the model (Jowett and Duncan, 2012).

3.5.3 Model algorithm

The IFIM commonly uses a univariate algorithm to relate the abiotic characteristics to actual habitat suitability (Conallin et al., 2010). The univariate derivation of the composite suitability index is criticized for being based on the assumption that organisms select each habitat variable independently, ignoring interactions and cumulative effects between them (Ahmadi-

Nedushan et al., 2006), such as the influence of velocity on substrate stability and composition (Shields, 1936). Multivariate statistical models, such as Generalized Additive Models (Milner et al., 2001) and Artificial Neural Networks (Gozlan et al., 1999), are alternative means of fitting the suitability data that are able to account for interactions between the variables and overcome the problem of independence (Ahmadi-Nedushan et al., 2006). Another, increasingly popular, approach is the use of "fuzzy logic" to define a set of rules that classifies suitability according to a combination of different environmental factors. It allows consideration of uncertain measurements and vague expert knowledge, as well as multivariate effects, without requiring the input parameters to be independent (Noack et al., 2013). With random forests we also applied a distribution modeling technique that is capable of modeling complex interactions among predictor variables and is considered to have one of the greatest discriminatory capacities (Elith et al., 2006; Cutler et al., 2007).

However, random forest and all other approaches are static and ignore more complex processes that are known to shape the distribution patterns of macrophytes, such as interspecific competition and feedbacks between the plants and the physical environment known as niche construction (Corenblit et al., 2009a). The latter has become very evident in the complex relationship between macrophytes and fine sediment, where macrophytes have been observed to create positive growth conditions through retention and stabilization of fine sediments, thereby also interacting with geomorphological processes (Schoelynck et al., 2012).

3.5.4 Model validation

Ecological modeling is of little value if the prediction is not tested against independent data (Olden et al., 2002). We therefore separated the study reach from the calibration reach and collected field data in two different years. The overall model prediction capacity at $Q = 0.3$ m^3/s was assessed as good using the threshold-independent AUC statistic. The binary prediction, and especially the rate of observed absences of the species that fall in pixels of predicted presences (the commission error rate, which equals 1 minus specificity), was less convincing, but can in part be explained by the low prevalence of the species. A distinction must be made between two different types of commission error: real commission errors, in which combinations of environmental conditions that are not within the species’ niche are falsely interpreted as suitable; and apparent commission errors, where absence represents a real feature of the species’ distributional ecology due to interspecific interactions and historical factors (Peterson, 1999). A high commission error is therefore common among species that show a low prevalence, and can be an indicator that the species has not yet conquered the whole of its potential niche. If this interpretation is correct, it would support the use of our model as a screening tool for identifying areas that are at higher risk of invasion.

We can only speculate about the causes of the spatial autocorrelation in the errors between observed and predicted species distribution: disregard of interactions between the predictor variables, omission of important predictors (temperature, nutrients), or ecological processes (dispersal, competition, niche construction) (Guisan and Thuiller, 2005). However, the model’s good predictive performance against independent data nonetheless proves the usefulness of the IFIM approach for predicting macrophyte distribution.

3.5.5 Other management options and conclusion

Mechanical methods are the most widely used measures for controlling aquatic macrophytes in both Portugal (Moreira et al., 1999) and Europe as a whole (Hussner et al., 2017). They allow for containment or eradication, depending on the specific technique and frequency of application (Madsen, 2000). Although often regarded as environmentally less harmful, the most common and effective measures like mowing are not species-specific and can both harm non-target aquatic biota and cause sediment resuspension (e.g. Habib and Yousuf 2014). Worldwide, chemical control is also applied. While proven very effective, even for eradicating nuisance weeds (Champion and Wells, 2014), herbicides will physiologically affect similar native aquatic plants and potentially also indirectly harm fish and invertebrates (Getsinger, 1998). The use of herbicides to control aquatic nuisance weeds is therefore severely restricted in various countries (especially in the EU). Biological measures also present a risk of off-target impacts, both directly and indirectly through alteration of the food web. Physical management methods are distinguished from mechanical techniques, because instead of the plants directly, it is their environment that is manipulated. Several physical techniques can be distinguished: dredging, drawdown, benthic barriers, shading or light attenuation, and nutrient inactivation (Madsen, 2000; Wersal et al., 2013). The control of nuisance weeds through flow regulation fits into the latter category, but has so far received little attention. Flushing flows have been successfully used to eradicate weeds in the Ebro river (Tena et al., 2013). However, frequency and magnitude of discharges (in the range of a 2-year flood) are not a viable option for intensive agricultural watersheds like the Sorraia, where both the side effects of the floodings and the competing water uses have to be considered.

Although most management techniques have some negative side effects on the ecosystem, so do the invasion and extreme growth of alien species. Maintaining minimum discharges in order to prevent channel encroachment may be an ecologically and financially advantageous addition to the range of commonly practiced control measures. We tested this approach by applying habitat suitability modeling techniques that are widely used to evaluate environmental flows and restoration measures aimed at fishes and invertebrates. Based on the specific habitat preferences of *Myriophyllum aquaticum*, it seems possible to set minimum flows that reduce the invader's habitat while simultaneously promoting that of autochthonous and less invasive aquatic species. This measure can be recommended with a high level of confidence, given that when the model was checked against independent data, it displayed a good level of accuracy in predicting species distribution.

3.6 References

Aguiar, F., & Ferreira, M. T. (2013). A review Plant invasions in the rivers of the Iberian Peninsula , south-western. Plant Biosystems, Vol. 147, pp. 1107–1119. https://doi.org/10.1080/11263504.2013.861539

Ahmadi-Nedushan, B., St-Hilaire, A., Bérubé, M., Robichaud, É., Thiémonge, N., & Bobée, B. (2006). A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications, 22(5), 503–523. https://doi.org/10.1002/rra.918

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Baattrup-Pedersen, A., & Riis, T. (1999). Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. Freshwater Biology, 42(2), 375–385. https://doi.org/10.1046/j.1365-2427.1999.444487.x

Barendregt, A., & Bio, A. M. F. (2003). Relevant variables to predict macrophyte communities in running waters. Ecological Modelling, 160(3), 205–217. https://doi.org/10.1016/S0304-3800(02)00254-5

Barko, J. W., Adams, M. S., & Clesceri, N. L. (1986). Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. Journal of Aquatic Plant Management, Vol. 24, pp. 1–10.

Benjankar, R., Tonina, D., & Mckean, J. (2015). One-dimensional and two-dimensional hydrodynamic modeling derived flow properties: Impacts on aquatic habitat quality predictions. Earth Surface Processes and Landforms, 40(3), 340–356. https://doi.org/10.1002/esp.3637

Bovee, K. D. (1982). A guide to stream habitat analysis using the instream incremental flow methodology. Instream Flow Information Paper. United States Fish and Wildlife Service. FWS/OBS-82/26, 12(82), 1–248.

Bovee, K. D. (1986). Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. USDI Fish and Wildlife Service.

Breiman, L. (2001). Random forests. Mach Learn, 45(1), 5–32. https://doi.org/10.1023/A:1010933404324

Brundu, G. (2014). Plant invaders in European and Mediterranean inland waters: profiles, distribution, and threats. Hydrobiologia, 746(1), 61–79. https://doi.org/10.1007/s10750-014-1910-9

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, 30(4), 492–507. https://doi.org/10.1007/s00267-002-2737-0

Cantor, S. B., Sun, C. C., Tortolero-Luna, G., Richards-Kortum, R., & Follen, M. (1999). A Comparison of C/B Ratios from Studies Using Receiver Operating Characteristic Curve Analysis. J Clin Epidemiol, 52(9), 885–892. https://doi.org/S089543569900075X [pii]

Carpenter, S. R., & Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes. Aquatic Botany, 26(C), 341–370. https://doi.org/10.1016/0304-3770(86)90031-8

Carr, G. M., Duthie, H. C., & Taylor, W. D. (1997). Models of aquatic plant productivity: a review of the factors that influence growth. Aquatic Botany, 59(3), 195–215.

Chambers, P. A., Prepas, E. E., Hamilton, H. R., & Bothwell, M. L. Current velocity and its effect on aquatic macrophytes in flowing waters. , 1 Ecological Applications § (1991).

Champion, P. D., & Wells, R. D. S. (2014). Proactive management of aquatic weeds to protect the nationally important Northland dune lakes , New Zealand. 139–142.

Conallin, J., Boegh, E., & Jensen, J. K. (2010). Instream physical habitat modelling types: an analysis as stream hydromorphological modelling tools for EU water resource managers. International Journal of River Basin Management, 8(1), 93–107. https://doi.org/10.1080/15715121003715123

Corenblit, D., Steiger, J., Gurnell, A. M., & Naiman, R. J. (2009). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: A niche construction perspective for riparian systems. Global Ecology and Biogeography, 18(4), 507–520. https://doi.org/10.1111/j.1466-8238.2009.00461.x

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random Forests for Classification in Ecology. Ecology, 88(11), 2783–2792. https://doi.org/10.1890/07-0539.1

Demars, B. O. L., & Edwards, A. C. (2009). Distribution of aquatic macrophytes in contrasting river systems: A critique of compositional-based assessment of water quality. Science of the Total Environment, 407(2), 975–990. https://doi.org/10.1016/j.scitotenv.2008.09.012

Den Hartog, C., & Van Der Velde, G. (1988). Structural Aspects of Aquatic Plant Communities. In J. J. Symoens (Ed.), Vegetation of inland waters (pp. 113–153). https://doi.org/10.1007/978-94-009-3087-2_4

Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Ferreira, M. T., & Moreira, I. S. (1995). The invasive component of a river flora under the influence of Mediterranean agricultural systems. The Invasive Component of a River Flora under the Influence of Mediterranean Agricultural Systems., 117–127.

Ferreira, M. T., & Moreira, I. S. (1999). River plants from an Iberian basin and environmental factors influencing their distribution. Hydrobiologia, 415, 101–107. https://doi.org/10.1023/A:1003837802366

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence / absence models. Environmental Conservation, 24(1), 38–49. https://doi.org/10.1017/S0376892997000088

Franklin, J. (2013). Species distribution models in conservation biogeography: Developments and challenges. Diversity and Distributions, 19(10), 1217–1223. https://doi.org/10.1111/ddi.12125

Franklin, P., Dunbar, M., & Whitehead, P. (2008). Flow controls on lowland river macrophytes: A review. Science of the Total Environment, 400(1–3), 369–378. https://doi.org/10.1016/j.scitotenv.2008.06.018

Gasith, A., & Resh, V. H. (1999). Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecology and Systematics, 30(1), 51–81.

Getsinger, K. D. (1998). Chemical Control Research in the Corps of Engineers. Engineer, 61–64.

Gómez, C. M., Pérez-Blanco, C. D., Batalla, R. J., G??mez, C. M., P??rez-Blanco, C. D., & Batalla, R. J. (2013). Tradeoffs in river restoration: Flushing flows vs. hydropower generation in the Lower Ebro River, Spain. Journal of Hydrology, 518(PA), 130–139. https://doi.org/10.1016/j.jhydrol.2013.08.029

Gozlan, R. E., Mastrorillo, S., Copp, G. H., & Lek, S. (1999). Predicting the structure and diversity of young-of-the-year fish assemblages in large rivers. Freshwater Biology, 41(4), 809–820. https://doi.org/10.1046/j.1365-2427.1999.00423.x

Gu, R., Montgomery, S., & Austin, T. Al. (1998). Quantifying the effects of stream discharge on summer river temperature. Hydrological Sciences, 43(6), 885–904. https://doi.org/10.1080/02626669809492185

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., … Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography, 24(3), 276–292. https://doi.org/10.1111/geb.12268

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. Ecology Letters, 8(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Habib, S., & Yousuf, A. R. (2014). Impact of mechanical deweeding on the phytophilous macroinvertebrate community of an eutrophic lake. Environmental Science and Pollution Research, 21(8), 5653–5659. https://doi.org/10.1007/s11356-013-2470-7

Halstead, J. M., Michaud, J., Hallas-Burt, S., & Gibbs, J. P. (2003). Hedonic Analysis of Effects of a Nonnative Invader (Myriophyllum heterophyllum) on New Hampshire (USA) Lakefront Properties. Environmental Management, 32(3), 391–398. https://doi.org/10.1007/s00267-003-3023-5

Hussner, A., Stiers, I., Verhofstad, M. J. J. M., Bakker, E. S., Grutters, B. M. C., Haury, J., … Hofstra, D. (2017). Management and control methods of invasive alien freshwater aquatic plants: A review. Aquatic Botany, 136, 112–137. https://doi.org/10.1016/j.aquabot.2016.08.002

Janauer, G. A., Schmidt-Mumm, U., & Schmidt, B. (2010). Aquatic macrophytes and water current velocity in the Danube River. Ecological Engineering, 36(9), 1138–1145. https://doi.org/10.1016/j.ecoleng.2010.05.002

Jones, J. I., Young, J. O., Eaton, J. W., & Moss, B. (2002). The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interaction between submerged plants and periphyton. Journal of Ecology, 90(1), 12–24. https://doi.org/10.1046/j.0022-0477.2001.00620.x

Jowett, I. G., & Duncan, M. J. (2012). Effectiveness of 1D and 2D hydraulic models for instream habitat analysis in a braided river. Ecological Engineering, 48, 92–100. https://doi.org/10.1016/j.ecoleng.2011.06.036

Jowett, I. G., Hayes, J. W., & Duncan, M. J. (2008). A guide to instream habitat survey methods and analysis. In Science And Technology. Retrieved from https://books.google.pt/books?id=mmqrPAAACAAJ

Koch, E. W. (2001). Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries, Vol. 24, pp. 1–17. https://doi.org/10.1007/BF02693942

Köhler, J., Hachoł, J., & Hilt, S. (2010). Regulation of submersed macrophyte biomass in a temperate lowland river: Interactions between shading by bank vegetation, epiphyton and water turbidity. Aquatic Botany, 92(2), 129–136. https://doi.org/10.1016/j.aquabot.2009.10.018

Lahoz-Monfort, J. J., Guillera-Arroita, G., & Wintle, B. A. (2014). Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography, 23(4), 504–515. https://doi.org/10.1111/geb.12138

Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. R News, 2(3), 18–22. Retrieved from http://cran.r-project.org/doc/Rnews/

Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. Ecography, 28(3), 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Madsen, J D, Chambers, P. a, James, W. F., Koch, E. W., & Westlake, D. F. (2001). The interaction between water movement, sediment dynamics andsubmersed macrophytes. Hydrobiologia, 444(1–3), 71–84. https://doi.org/10.1023/A:1017520800568

Madsen, John D. (2000). Advantages and Disadvantages of Aquatic Plant Management Techniques. In Lakeline (Vol. 20). Retrieved from ENGINEER RESEARCH AND DEVELOPMENT CENTER VICKSBURG MS ENVIRONMENTAL LAB website: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.513.3522&rep=rep1&type=pdf

Mainstone, C. P., & Parr, W. (2002). Phosphorus in rivers - Ecology and management. Science of the Total Environment, 282–283(October), 25–47. https://doi.org/10.1016/S0048-9697(01)00937-8

Mathur, D., Bason, W. H., Purdy Jr., E. J., & Silver, C. A. (1985). A Critique of the In stream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Sciences, 42(4), 825–831. https://doi.org/10.1139/f85-105

Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: A synthesis. Freshwater Biology, 46(12), 1833–1847. https://doi.org/10.1046/j.1365-2427.2001.00861.x

Moreira, I., Ferreira, M. T., Monteiro, A., Catarino, L., & Vasconcelos, T. (1999). Aquatic weeds and their management in Portugal: insights and the international context. Hydrobiologia, 415, 229–234.

Nikora, V., Larned, S., Nikora, N., Debnath, K., Cooper, G., & Reid, M. (2008). Hydraulic Resistance due to Aquatic Vegetation in Small Streams: Field Study. Journal of Hydraulic Engineering, 134(9), 1326–1332. https://doi.org/10.1061/(ASCE)0733-9429(2008)134:9(1326)

Noack, M., Schneider, M., & Wieprecht, S. (2013). The habitat modelling system CASiMiR: a multivariate Fuzzy approach and its applications. Ecohydraulics: An Integrated Approach, 75–91.

O’Hare, M. T., Baattrup-Pedersen, A., Nijboer, R., Szoszkiewicz, K., & Ferreira, M. T. (2006). Macrophyte communities of European streams with altered physical habitat. Hydrobiologia, 566(1), 197–210. https://doi.org/10.1007/s10750-006-0095-2

Olden, J. D., Jackson, D. A., & Peres-Neto, P. R. (2002). Predictive models of fish species distributions: a note on proper validation and chance predictions. Transactions of the American Fisheries Society, 131(September 2012), 329–336. https://doi.org/10.1577/1548-8659(2002)131<0329:PMOFSD>2.0.CO;2

Perona, P., Camporeale, C., Perucca, E., Savina, M., Molnar, P., Burlando, P., & Ridolfi, L. (2009). Modelling river and riparian vegetation interactions and related importance for sustainable ecosystem management. Aquatic Sciences, 71(3), 266–278. https://doi.org/10.1007/s00027-009-9215-1

Peterson, A. T. (1999). Conservatism of Ecological Niches in Evolutionary Time. Science, 285(5431), 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Pollen-Bankhead, N., Thomas, R. E., Gurnell, A. M., Liffen, T., Simon, A., & O’Hare, M. T. (2011). Quantifying the potential for flow to remove the emergent aquatic macrophyte Sparganium erectum from the margins of low-energy rivers. Ecological Engineering, 37(11), 1779–1788. https://doi.org/10.1016/j.ecoleng.2011.06.027

Pysek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. Taxon, 53(1), 131–143. https://doi.org/10.2307/4135498

Raleigh, R. F., Miller, W. J., & Nelson, P. C. (1986). Habitat suitability index models and instream flow suitability curves: Chinook Salmon. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.122) (Vol. 82). Retrieved from http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA322912

Riis, R., & Biggs, B. J. F. (2001). Distribution of macrophytes in New Zealand streams and lakes in relation to disturbance frequency and resource supply - a synthesis and conceptual model. New Zealand Journal of Marine and Freshwater Research, 35(2), 255–267. https://doi.org/10.1080/00288330.2001.9516996

Riis, T., & Biggs, B. J. F. (2003). Hydrologic and hydraulic control of macrophyte establishment and performance in streams. Limnology and Oceanography, 48(4), 1488–1497. https://doi.org/10.4319/lo.2003.48.4.1488

Riis, Tenna, Suren, A. M., Clausen, B., & Sand-Jensen, K. (2008). Vegetation and flow regime in lowland streams. Freshwater Biology, 53(8), 1531–1543. https://doi.org/10.1111/j.1365-2427.2008.01987.x

Schmolke, A., Thorbek, P., DeAngelis, D. L., & Grimm, V. (2010). Ecological models supporting environmental decision making: A strategy for the future. Trends in Ecology and Evolution, 25(8), 479–486. https://doi.org/10.1016/j.tree.2010.05.001

Schoelynck, J., De Groote, T., Bal, K., Vandenbruwaene, W., Meire, P., & Temmerman, S. (2012). Self-organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation. Ecography, 35(8), 760–768. https://doi.org/10.1111/j.1600-0587.2011.07177.x

Shields, A. (1936). Anwendung der Aehnlichkeitsmechanik und der Turbulenzforschung auf die Geschiebebewegung. Technology, 26(1), 26.

Steffen, K., Leuschner, C., Mueller, U., Wiegleb, G., & Becker, T. (2014). Relationships between macrophyte vegetation and physical and chemical conditions in northwest German running waters. Aquatic Botany, 113, 46–55. https://doi.org/10.1016/j.aquabot.2013.10.006

Steffler, P., & Blackburn, J. (2002). River2D Two-Dimensional Depth Averaged Model of River Hydrodynamics and Fish Habitat Introduction to Depth Averaged Modeling and User ' s Manual by. Software Manual, 1-.

Tena, A., Ksiaszek, L., Vericat, D., & Batalla, R. J. (2013). Assessing the geomorphic effects of a flushing flow in a large regulated river. River Research and Applications, 29(7), 876–890. https://doi.org/10.1002/rra.2572

VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., & Storlie, C. (2014). SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modelling exercises. Retrieved from https://cran.r-project.org/package=SDMTools

Vereecken, H., Baetens, J., Viaene, P., Mostaert, F., & Meire, P. (2006). Ecological management of aquatic plants: effects in lowland streams. In Macrophytes in Aquatic Ecosystems: From Biology to Management (pp. 205–210). Springer.

Wersal, R. M., Madsen, J. D., & Gerard, P. D. (2013). Survival of parrotfeather following simulated drawdown events. Journal of Aquatic Plant Management, 51(2007), 22–26.

4 MODEL-BASED RECONSTRUCTION OF THE SUCCESSION DYNAMICS OF A LARGE RIVER FLOODPLAIN

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4.1 Abstract

Most large rivers in Europe and North America suffered flow regulations and channelization in the 19th and 20th centuries. To study the effects of the altered site conditions on the development of floodplain vegetation and create a benchmark map for their restoration we calibrated and applied a dynamic floodplain vegetation model that accounts for the processes recruitment as well as morphodynamic disturbance and physiologic stress on vegetation to reconstruct the succession dynamics of the floodplain vegetation of a segment of the Rhine river from shortly after it was channelized (1872) until today (2016). The model calibration was based on historical maps and hydrologic data.

Our simulation demonstrated a steady, one-way progression of the vegetation communities toward mature phases without regression to younger stages. It was possible to attribute this development to a lack of morphodynamic disturbances strong enough to reset succession and to identify physiological stress caused by long inundations periods as the most relevant controlling factor of succession. The resulting vegetation distribution (2016) can be considered an estimation of the potential natural vegetation (PNV) under altered site conditions.

The good agreement of the model results with an expert-based PNV map showed that our approach is a good alternative to create benchmark maps for floodplain conservation and restoration projects. From a research and practitioners' viewpoint it has the big advantage over the traditional approach that it allows to analyze different points in time as well as to be comprehensive and reproducible.

Keywords: riparian vegetation, large rivers, dynamic modeling, succession, historic development

4.2 Introduction

Natural river floodplains belong to the most productive and biodiverse ecosystems worldwide (Ward et al., 1999). One of the reasons is that successional sequences are repeatedly rejuvenated and reset by hydro-geomorphologic disturbances, creating a continuously shifting mosaic of habitat patches (Pringle et al., 1988; Stanford et al., 2005). Most large temperate rivers however are heavily modified through flow regulation as well as straightened and stabilized channels (Dynesius and Nilsson, 1994; Buijse et al., 2002; Tockner et al., 2009). This leads to a replacement of dynamic geomorphological processes (e.g. avulsion, meandering, braiding) by one-way developments (e.g. riverbed degradation, floodplain siltation) (Kikyo et al., 1999; Petts and Gurnell, 2005) as well as a decrease of hydrodynamic variability and disturbance in the riparian zone (Church, 1995; Magilligan and Nislow, 2005). The understanding of the effects of altered site conditions on habitat configuration across different spatial and temporal scales is important for river conservation and restoration as well as the study of floodplain ecology in general (Ward and Stanford, 1995; Vaughan et al., 2009; Gumiero et al., 2013). A challenge in this context is that reference reaches that would allow investigation of natural succession dynamics over different time spans are nearly non-existent in large rivers (Whited et al., 2007). Moreover, the modification of 90% of the floodplains in Europe and North America through agriculture or forestry (Tockner and Stanford, 2002; Buijse et al., 2005) makes it difficult to distinguish the effects of altered site condition on the actual vegetation. In general vegetation records for historical analyses are rare and often of low quality (Swetnam et al., 1999).

Modeling approaches based only on physical habitat parameters can predict the vegetation at a location without the effect of direct anthropogenic land-use change (Ricotta et al., 2000; Kelly et al., 2005) and have been applied to produce benchmarks for nature conservation (Rosati et al., 2008; Arco Aguilar et al., 2010) or to compare the outcomes of different types of management (Barnes et al., 1982). Dynamic models also allow to simulate succession (Taylor et al., 2009) and reconstruct historic developments (Li, 2000; Wimberly, 2002; Keane et al., 2006). In the past, many different models have been developed to predict the vegetation distribution in floodplains based on environmental factors (Franz and Bazzaz, 1977; Friedman and Auble, 1999; Lenders et al., 2001; Jungwirth et al., 2002; Aggenbach and Pelsma, 2003; Runhaar, 2003) or more recently to simulate their development over time (Camporeale and Ridolfi, 2006; Benjankar et al., 2011; García-Arias and Francés, 2016; Oorschot et al., 2016). Yet, the reconstruction of the succession dynamics of a large river floodplain after it suffered the typical reduction of hydro-geomorphological disturbances has never been attempted.

In this study we therefore parameterized a dynamic floodplain vegetation model based on historical maps and hydrologic data to reconstruct floodplain vegetation succession of a segment of the Rhine river, from shortly after it was straightened and channelized (1872) until today (2016). Our objectives were to investigate the succession trajectory under altered site conditions in a high temporal and spatial resolution, identify the ecological key processes that control the succession and to produce a baseline map of the potential natural vegetation (PNV) for restoration and conservation projects.

4.3 Methodology

4.3.1 Study Area

The Rhine River is one of the largest rivers in Central Europe with a length of about 1.230 km and a catchment area of approximately 185.300 km^2. Our study area lies in the Upper Rhine region where the nival discharge regime is strongly influenced by snow-melting in the Alps and the highest floods occur in summer (Belz and Frauenfelber-Kääb, 2007). Until the beginning of the 19th century the Upper Rhine could still be considered in natural condition (Gallusser and Schenker, 1992) and has been classified as a highly dynamic, island-dominated, anabranching river system (Gurnell and Petts, 2002; Herget and et al., 2005). But in the course of the 19th century, the Upper Rhine River was transformed into a single-thread channel by cutting off meander bends and by building groins and bank revetments (Bernhardt, 2000). In the 20th century the river regulation intensified through the construction of 10 hydropower plants in the main channel or in artificial side channels (Dister et al., 1990). During this time industry and settlements also expanded in the study area (Habersack and Piégay, 2007). The study area is the “Raststatter Rheinaue”, a nature reserve on the eastern, German side of the floodplain of a 9-km length segment of the Upper Rhine River downstream from the Iffezheim dam to the confluence of the river Murg (Rhine km 335.8 – 345, 114–110 m a.s.l., Figure 13). It is limited by flood dykes towards the east and covers a total area of approximately 645 ha (including water bodies).

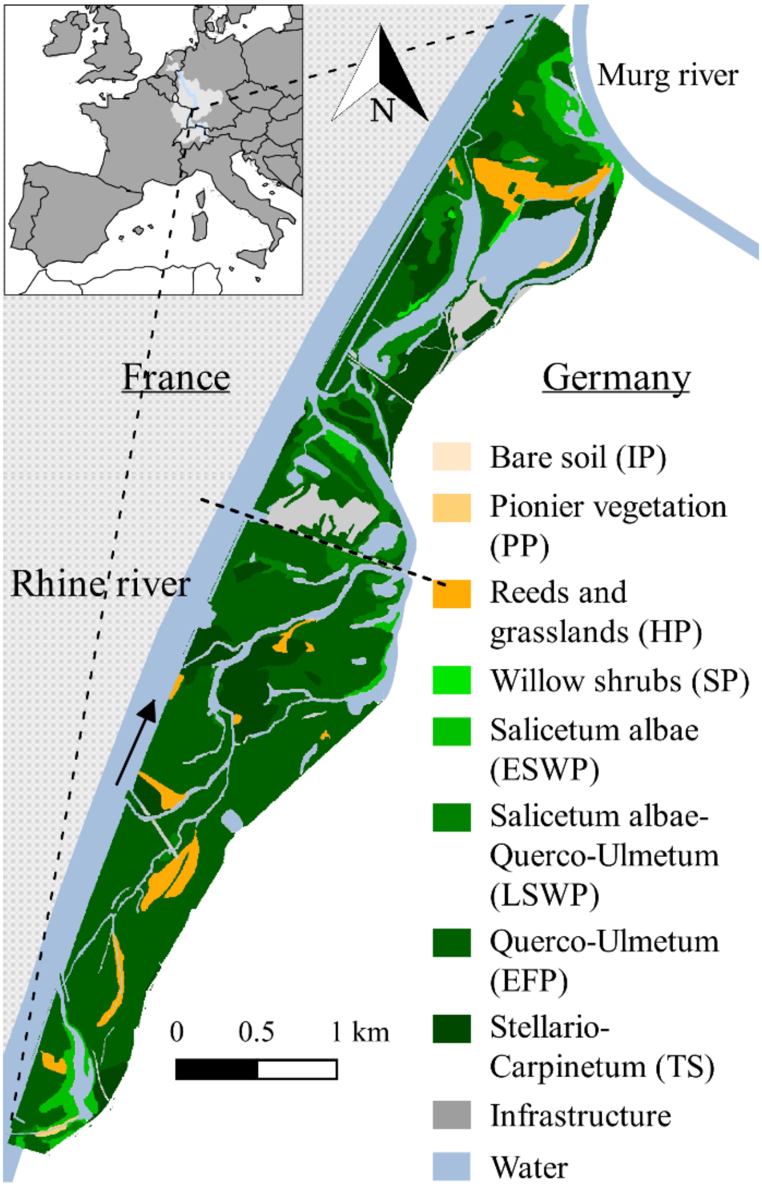

Figure 13: Upper left corner: Location of the study area in central Europe (dark grey) and the Rhine basin (light grey); Rest: Location of the study area along the eastern (German) side of the Rhine river and results of the expert-based estimation of the potential natural vegetation (PNV) from the year 2016. The PNV is expressed as vegetation communities and the corresponding succession phase (in brackets). The division in calibration and validation data is indicated by the dashed line perpendicular to the river channel (point of intersection with the Rhine river: 48°53'13.7"N 8°08'12.1"E)

4.3.2 Material and Data

Historic maps

Since the Upper Rhine has been the border between France and Germany for centuries, the riverine landscape has been the subject of many historical drawings and maps. At the beginning of the 19th century detailed maps were produced for the planning of the river straightening. These maps indicated the river bottom along the thalweg (line along the deepest points of the riverbed), the situation of water bodies, islands and gravel/sand bars within the aquatic area, as well as land uses in the floodplain (grasslands, forests, croplands and settlements). Our work is based mainly on four historical maps from that time (1816, 1838, 1852, 1872) that were georeferenced and classified in natural (natural water body, gravel/sand bar, grassland and forest) or anthropic (regulated water body, artificial water body, cropland, settlement, industry and gravel pit) habitat categories (for details see: Diaz-Redondo et al., 2017).

Expert PNV-Map

For model calibration and validation an expert-based map of the potential natural vegetation (PNV) was produced. Initially 291 similar vegetation patches were delineated visually on the basis of orthophotos (2009, 1 m resolution) and homogenous morphology (DEM, 1 m resolution). These patches were then further refined, and their PNV-type identified through field visits in summer 2016 and winter 2017. The identification of the PNV-type was mainly guided by indicator species (Table B 1). Where the actual vegetation showed a high degree of transformation through forestry and agriculture the extrapolation of the PNV-type in the field was supported by maps of the soil-type and height above mean-water.

Seven vegetation types were distinguished (Dister, 1980) and assigned to a succession phase (Table B 1 and Figure 13): pioneer vegetation, reeds and natural grasslands, willow shrubs, Salicitum albae, Salicitum albae - Querco-Ulmetum, Querco-Ulmetum and Stellario-Carpinetum.

Discharge data and Hydrodynamic model

The analysis of the flow regime of the study area for the whole simulation period is based on the Maxau gauging station (Rhine km 362.3) which has the longest continuous record of daily discharge (1921 – today) and also records of the annual low, mean and high discharges for the period 1872 -1921 (Diaz-Redondo et al., 2017). A two-dimensional hydrodynamic model (SRH-2D; Lai, 2008) of the Rhine river and its eastern floodplain was set up. The model bathymetry is based on a high-resolution (0.5 m) DEM (July 2016, German Federal Institute of Hydrology) supplemented by longitudinal profiles and cross-sections through the main water bodies in the study area (Díaz-Redondo et al., 2018). The model was calibrated by adjusting Manning's roughness coefficients (separately for the main channel and the floodplain) and comparing modeled and measured water surface elevations for 6 flow rates between MQ and HQ10.

The calibrated model was then used to determine the hydrodynamic and hydrologic parameters (water level, shear stress, flood duration) required as an input for the dynamic vegetation model for 14 flow rates ranging from 609 m³/s to 5300 m³/s (Table C 2). The modeled discharges were selected based on characteristic return periods and completed to better represent the flow duration curve around 2000 m³/s when the large-scale flooding of the floodplain starts.

4.3.3 Dynamic succession model

We used the dynamic, rule-based floodplain vegetation model CASiMiR (Egger et al., 2013; freely available under www.casimir-software.de) to simulate the succession in the study area from 1872 to 2016. The riparian vegetation is represented in succession lines and their respective succession phases (Table A 2). Three different succession lines were distinguished for the study area. The sand aggradation line develops on sediments from medium sand to sandy silt in flood zones with medium flow velocities. The silt aggradation line is limited to oxbows and terrain depressions where due to low flow rates mainly silt is deposited. The different textures of the substrate have implications for vegetation development, for example through differences in the water holding capacity (Saxton et al., 1986) which is why the expert rules of each succession line differ (Table A 2, Table A 4 and Table A 5).

For grasslands and agriculture areas a secondary succession line (Horn, 1974) was defined. Each succession line was further divided into succession phases according to Naiman et al. (2005) and Egger et al. (2013). The initial phase (IP) starts when the seedlings begin to colonize the bare sediments. It is followed by the pioneer phase (PP) characterized by relatively sparse vegetation of ruderal or stress-tolerant species. In the first phase of the transition stage (herb phase, HP) herbaceous short-lived species dominate but pioneer shrubs can also grow already. When the woody species grow above the herbs the shrub phase (SP) is reached. Later when pioneer trees like *Salix alba* and *Populus nigra* replace the shrubs as the dominant life form the early successional woodland phase (ESWP, Salicetum albae) is reached. It is followed by the late successional woodland phase (LSWP, Salicetum albae - Querco-Ulmetum) which experiences less disturbances and is characterized by the gradual transition from pioneer trees to the first hardwood species (*Fraxinus excelsior*, *Quercus robur*, *Ulmus laevis*). In the established forest phase (EFP, Querco-Ulmetum) the hardwood forest dominates. The terminal stage (TS, Stellario-Carpinetum) is characterized by lower biomass production but larger standing biomass. Competitive woody and long-lived species dominate. The starting condition of the model (vegetation distribution in 1872, Figure A 2) was derived from the analysis of the chronological sequence of the forest, gravel and water surfaces on historical maps (1816, 1838, 1852, 1872) of the area (see Table A 1, and Diaz-Redondo et al., 2017). Areas that were forested from 1816 through 1872 were assigned to EFP (sand aggradation line). Areas that changed from gravel in 1838 or 1852 to forest in 1872 were assigned to ESWP (sand aggradation line) and those that changed from water to forest were considered ESWP (silt aggradation line). Gravel- and sandbanks in 1872 were considered IP. Grasslands and agriculture areas in 1872 were defined as the beginning of the secondary succession (HP). Lateral arms and oxbows that vanished on historical maps between 1872 and 1893 (only geomorphological changes observed after 1872) were considered as “shallow water” (SW) in the silt aggradation line.

The dynamic modules of the model are recruitment, morphodynamic disturbance (indicated by shear stress) and physiological disturbance (indicated by flood duration) (Table A 4 and

Table A 5). Their behavior is based on rules describing the age spans of each succession phase, min and max water table for recruitment as well as critical values for disturbance indicators slowing down or setting back the succession (Egger et al., 2013). Each year the recruitment module checks for bare soils in the bank and floodplain zone as well as the water levels that allow seedling survival (Table A 3). The bank zone was defined as the area between the level of the mean water in the months of May and June (1257 m³/s; lower limit) and the water level, which is reached at 2000 m³/s (upper limit). Higher lying areas (up to HQ100) were assigned to the floodplain zone. The disturbance module checks whether the critical values of the disturbance indicators are surpassed (Table A 4 and Table A 5). If no disturbances occur, the vegetation becomes older (one-year step) and eventually progresses to the next succession phase. If the critical disturbance values for a succession phase are exceeded the vegetation will be set back according to the rules. The indicator “shear stress” was divided into five intensity classes: very low (0.1-2 N/m²), low (2-5 N/m²), medium (5-50 N/m²), high (50-200 N/m²) and very high (> 200 N/m²). “Shear stress” raster maps were assigned from the modeled flow rates (Table C 1) to each particular year of the scenario run (1872-2016) based on the years’ maximum discharge. The flooding stress was evaluated for the growing period (183 days, April - September) and also divided into five intensity classes: very low (0-5 days flooded), low (5-20 days), medium (20-70 days), high (70-120 days) and very high (120-183 days). Five representative years (dry, medium wet, wet, very wet and extreme wet) from the period 1921-2016 were selected based on their maximum, mean and minimum discharge (Table C 1). For the calculation of the flood duration raster of each representative year we attributed to the flooded area of each water level of the 14 modeled discharges (Table C 2) the number of days that they were exceeded during the growing period through analyzing the year’s hydrograph. The final raster was then composed by the flooded area of each discharge and their number of days exceeded, interpolated proportional to a cell’s elevation. The remaining years of the whole modeling period were then assigned to one of the representative years based on the number of days with a discharge greater than 2000 m³/s (= start of large-scale flooding of the floodplain). The extremely wet year (1999) occurred only once. For the period 1872-1921 only records of the annual low, mean and high discharges were available. For this period, we assigned a representative years' hydrograph using a decision tree model calibrated for the years 1921-2016.

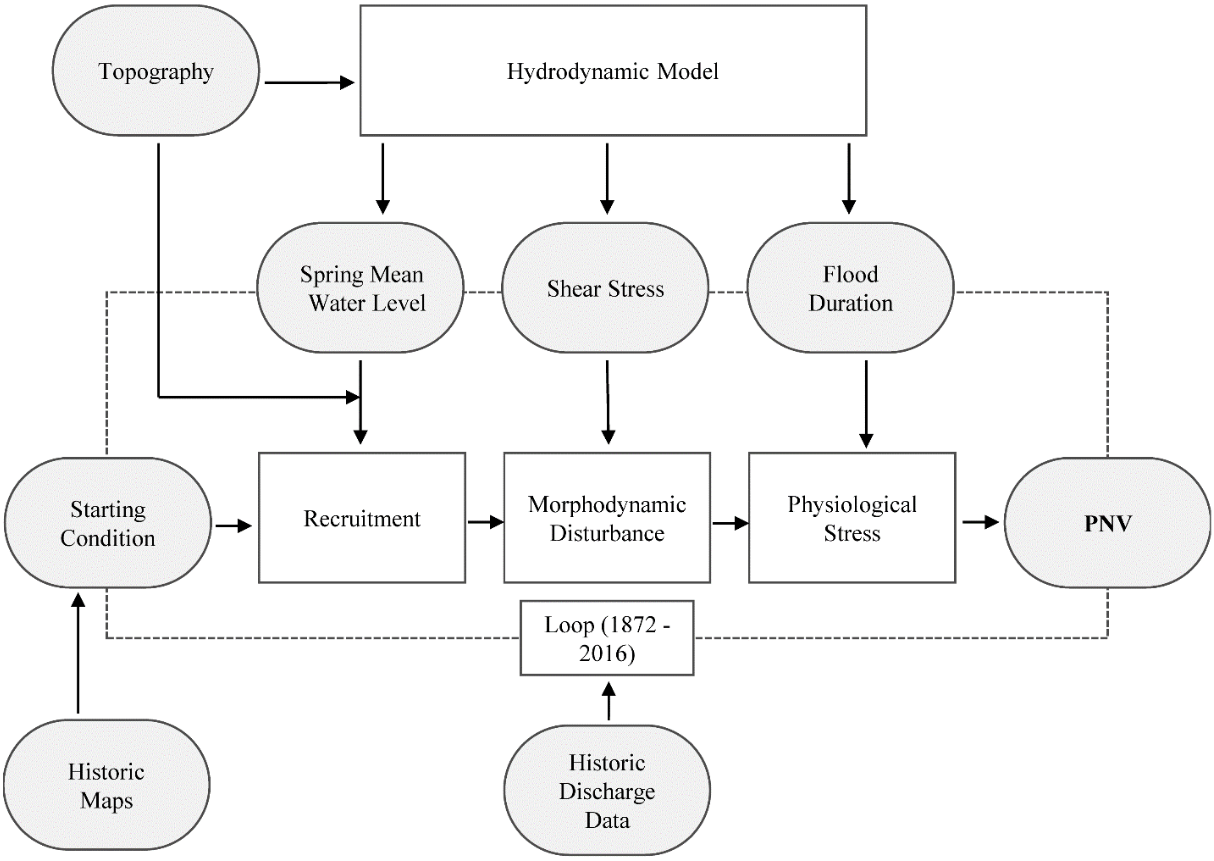

Figure 14: Flow diagram of the CASiMiR Vegetation model (adapted from Egger et al., 2013). Grey rectangles with rounded corners are model inputs or results, the white rectangles represent the dynamic modules of the model

4.3.4 Model calibration and validation

The model was calibrated and validated against the expert-based PNV-map (Figure 13). To ensure independence it was divided roughly in half perpendicular to the river channel along a road. The expert-rules were first estimated based on expert knowledge and then further calibrated manually using the downstream part until the model results for the year 2016 matched the PNV-map best. The validation was done with the upstream part of the study area. For the assessment of the agreement between the PNV-map and the model results we used a fuzzy set approach with the free software Map Comparison Kit (Visser and De Nijs, 2006). The application of fuzzy sets in map comparisons allows for the consideration of similarities as well as spatial proximity between classes (van Vliet et al., 2013). The distance decay function for the fuzziness of locations, that defines the influence of neighboring cells on the cell under comparison, was assumed to be linear with a slope of 0.5 over a distance of 4 cells (20 m). The similarity of plant communities along the successional gradient (Initial Phase -> Terminal Stage) was defined in a similarity table (Table 4). Based on the fuzzy sets we calculated the average similarity (AS; fuzzy equivalent to the fraction of correctly classified instances) globally and for each succession phase.

For a sensitivity analysis of our simulation regarding the main controlling factors of succession we additionally validated two alternative model runs a) only considering morphodynamic disturbance and b) only considering physiological disturbance.

		Succession Phase							
		IP	PP	HP	SP	ESWP	LSWP	EFP	TS
PNV-Type	Bare Soil (IP)	1	0.9	0.2	0	0	0	0	0
	Pioneer Vegetation (PP)	0.9	1	0.8	0	0	0	0	0
	Reeds and grasslands (HP)	0.2	0.8	1	0.5	0	0	0	0
	Willow shrubs (SP)	0	0	0.5	1	0.8	0.2	0	0
	Salicetum albae (ESWP)	0	0	0	0.8	1	0.8	0.2	0
	Salicetum albae-Querco-Ulmetum (LSWP)	0	0	0	0	0.8	1	0.8	0.2
	Querco-Ulmetum (EFP)	0	0	0	0	0.2	0.8	1	0.8
	Stellario-Carpinetum (TS)	0	0	0	0	0	0.2	0.8	1

Table 4: Contingency table describing the similarities along the successional gradient (IP -> TS) between plant communities (1 = equal; 0 = completely different)

4.3.5 Analyses the Trajectories of the succession dynamics

The trajectories of succession dynamics were interpreted through the analysis of the balance of regression versus progression processes along two time periods (as described in Diaz-Redondo et al., 2017; Whited et al., 2007) through the intersection of the model results for the year 1872 (starting condition), 1933 (mid-time) and 2016 (end result). Three categories were distinguished: changeless, progression, regression.

4.4 Results

The PNV of the study area considering the altered disturbance regime (model result for 2016, Figure 15) shows a landscape dominated by hardwood forests (EFP and TS, 56%) and forests in transition from softwood forests to hardwood forests (LSWP, 36%). Softwood forests (ESWP) only remain on 6.5% of the study area and early succession phases (IP, PP, HP, SP) on around 8%.

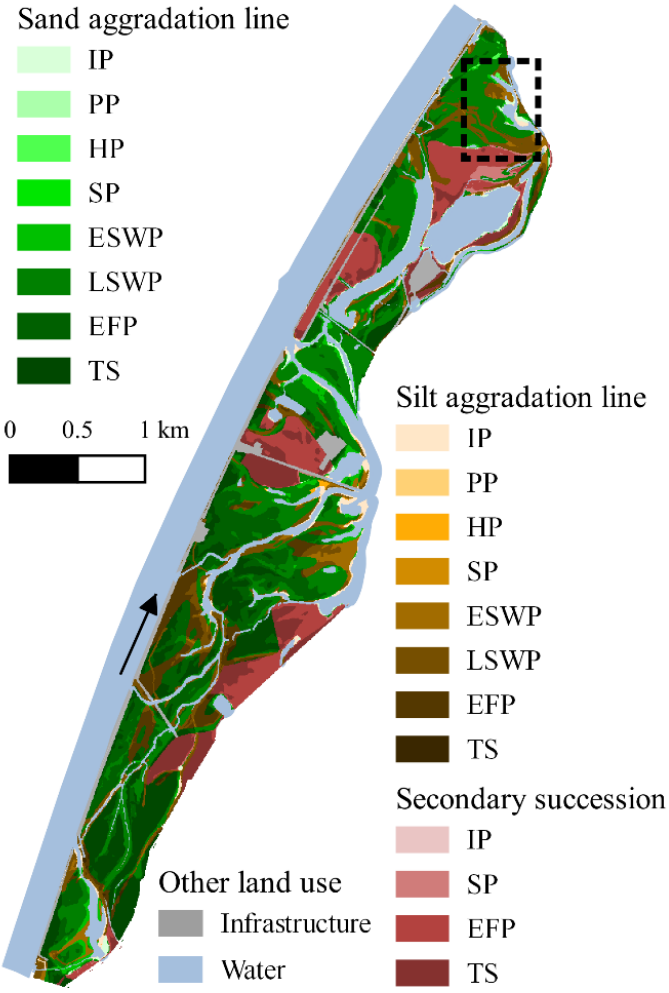

Figure 15: Simulated PNV of the study area for the year 2016. The rectangle in the upper right corner indicates the region that is shown in a higher temporal resolution in Figure 17

The analyses of the area development of the main succession phases between 1872 and 2016 (Figure 16) demonstrated that the areas covered by early succession phases shrank fast from initially over 36% (1872) to 13% (1910) and by the end of the simulation period to around 8%. ESWP was the dominant succession phase in 1872 covering over 55% of the study area. After only 35 years it decreased to around 20% and in 2016 only 6.5% remained. LSWP first appeared after 35 years evolving from ESWP. By 1910 it covered around 50% of the study area but shrank to around 30% by 2016. EFP and TS were only found on around 11% of the study area in 1872. They gradually increased to become the most dominant succession phases in 2016 covering over 50%.

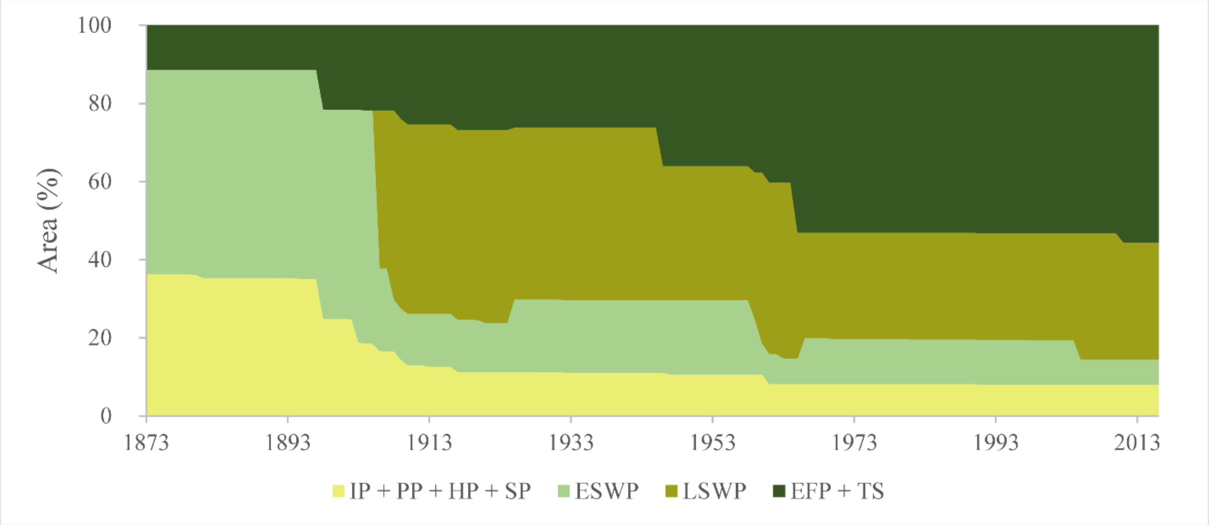

Figure 16: Simulated area development of the main succession phases (the different succession series were summed up)

A visualization of the succession dynamic in a 10-yer resolution (Figure 17) revealed small scale (5m spatial resolution) changes of the vegetation pattern. Early succession phases and ESWP only remain around the margins of the water bodies were the disturbance frequency and magnitude are the highest.

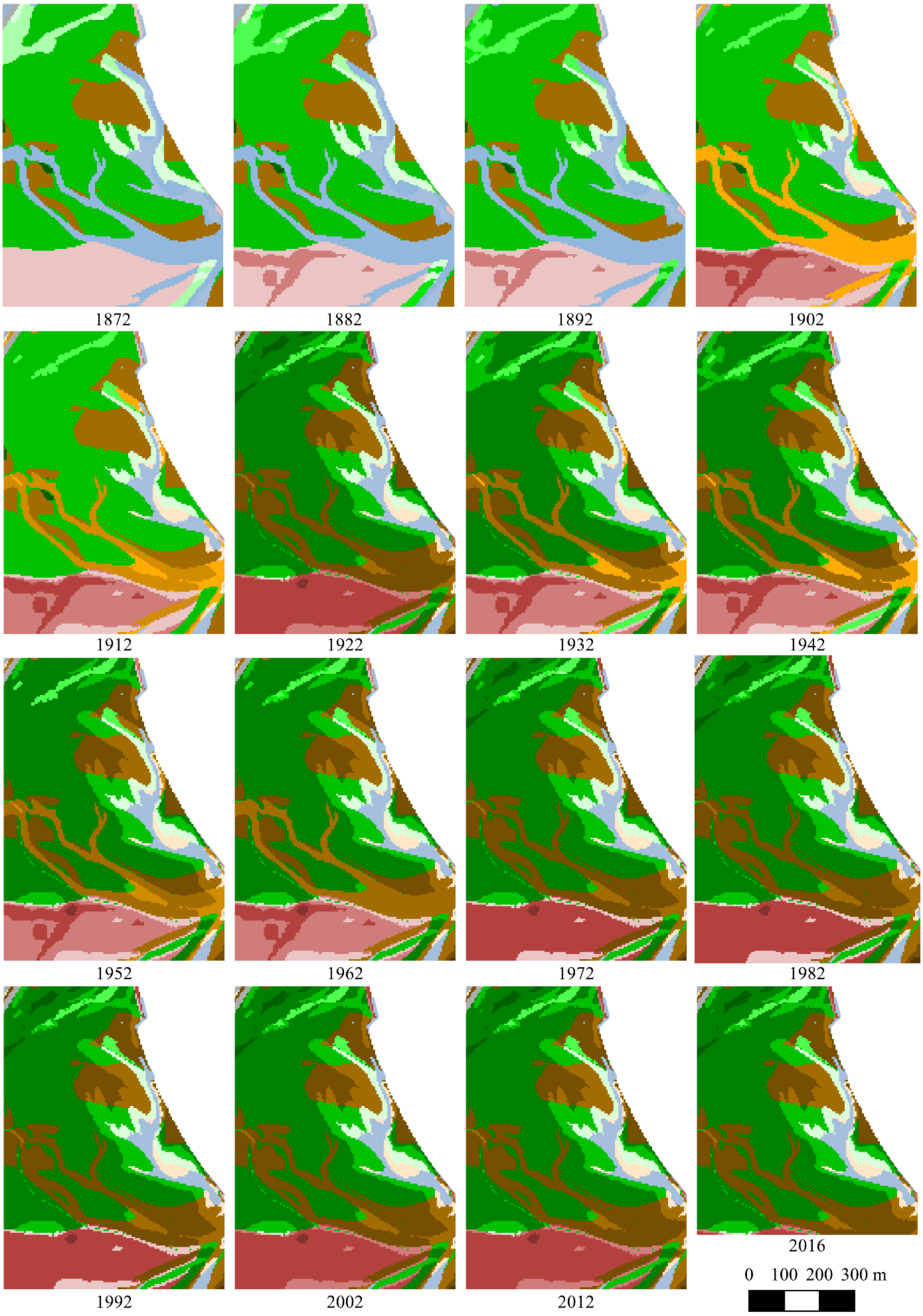

Figure 17: Model results for a selected region of the study area (see Figure 15) in a 10-year resolution (for the legend see also Figure 15)

The results of the main habitat change trajectories demonstrate a clear dominance of progression over regression processes. From 1872 to 1933 80.11% of the habitats progressed to more mature succession phases, 18.7% remained changeless and only 1.19% of the habitats were affected by regression. From 1944 to 2016 the progression slows down (52.69%) and more habitat remained changeless (45.91%). The regression rate continued very low (1.13%).

Validation

Considering the fuzzy rules, the overall average similarity of our prediction and the expert-based field map was 0.81. The early succession phases (IP, PP, HP, SP) had low agreements with AS values between 0 and 0.17. The ESWP showed general good agreement but differed between sand aggradation (AS = 0.74) and silt aggradation line (AS = 0.5). LSWP also matched well with the expert-based PNV map (AS = 0.74). The mature succession phases EFP and TS had the best agreement with AS values between 0.82 and 0.96 (Table 5).

Our sensitivity analyses regarding the disturbance indicators identified the physiological stress indicated by “flood duration” as the main controlling factor of succession. If only physiological stress is considered, and the effect of morphodynamic disturbance on the vegetation neglected the average similarity with the expert-based PNV-map remained 0.81. Without the consideration of the physiological stress on the other hand earlier succession phases and ESWP disappeared completely and the succession in the whole study area progressed until EFP and TS. In this scenario the average similarity with the expert-based PNV-map dropped to 0.73.

	Succession phase	AS per category	Area (ha)	Area (%)
Sand Aggradation Line	IP	0.05	1.13	0.39
	PP	0.00	0.01	0.00
	HP	0.12	0.09	0.03
	SP	0.00	0.00	0.00
	ESWP	0.74	5.16	1.77
	LSWP	0.74	55.61	19.08
	EFP	0.93	63.17	21.67
	TS	0.82	61.16	20.98
Silt Aggradation Line	IP	0.00	5.45	1.87
	PP	0.00	0.00	0.00
	HP	0.04	0.53	0.18
	SP	0.00	0.01	0.00
	ESWP	0.50	8.95	3.07
	LSWP	0.74	27.60	9.47
	EFP	0.92	23.59	8.09
	TS	0.81	0.89	0.31
Secondary Succession	HP	0.17	0.14	0.05
	SP	0.01	0.88	0.30
	EFP	0.96	15.84	5.43
	TS	0.80	21.30	7.31

Table 5: Validation results: Average Similarity (AS) of each succession phase with the expert-based PNV map considering similarities along the successional gradient (Table 4) and the fuzziness of location as well as the areas (ha, %) of each succession phase

4.5 Discussion

The simulation of the succession dynamics in our study area from shortly after it suffered the typical changes of site conditions in the 19th century until today demonstrates a steady, one-way progression of the vegetation communities toward mature phases. A trend that has also been observed by other studies only based on historic data and aerial photos (Tockner and Stanford, 2002; Hohensinner et al., 2004; Ollero, 2010; Diaz-Redondo et al., 2017). The advantage of our modeling approach lies in the high temporal (1-year time step), spatial (5 m) and ecological resolution (succession lines and phases) as well as in the possibility to analyze the influence of the assumed key drivers. The steady habitat aging of large river floodplains has been mainly attributed to an impediment of geomorphologic dynamics through bank stabilization and flow regulation (Florsheim et al., 2008; Hohensinner et al., 2014). Correspondingly, our sensitivity analyses indicated that in our study area morphodynamic disturbances on vegetation are not strong enough to reset the succession phases. Succession is only controlled by "flood duration" which is able to slow it down in some areas around the margins of waterbodies where only *Salix alba* is adapted to resist the strong physiological stress caused by long flood durations (Glenz et al., 2006).

Due to the temporal dynamics and complexity of the riparian ecosystem the reconstruction of the succession with the CASiMiR model is based on several assumptions and simplifications. Biotic factors were summed up in succession lines and phases that have been observed to show distinct responses to disturbances (Kovalchik and Clausnitzer, 2001; Naiman et al., 2005). The model starting condition (vegetation distribution in 1872) has to be regarded with some degree of uncertainty. The low resolution of the historic maps and the short time span covered by them (1816-1872) only allowed a classification of the flood plain forests as ESWP or EFP. The unrealistic lack of LSWP in 1872 explains its sudden appearance (progression from ESWP without disturbance) at around 1910 in our simulation (Figure 16). Also, the spatial delineation of the succession lines from historic land cover transitions can only be considered an estimation. The recruitment module is an adaptation of the "recruitment box model" which assumes the spring mean water level as the main controlling factor of dispersal and seedling survival (Mahoney and Rood, 1998). The disturbance module is based on the observation that in floodplains morphodynamic disturbance and physiological stress caused by floods are the main processes to control the survival and succession of vegetation (Bendix and Hupp, 2000; Naiman et al., 2008; Merritt et al., 2010). Regarding the morphodynamic disturbance indicator “shear stress” we only accounted for the maximum discharge registered in each year which has been recognized as the most relevant event (Junk et al., 1989; Friedman and Lee, 2002). The fixed topographic input of the simulation we consider a justified simplification of the complex hydro-geomorphological processes normally occurring within the floodplain (Gurnell, 2016) because the artificial suppression of these dynamics is part of the altered site condition we wanted to model. Also, the resolution of the temporal dynamics regarding flood duration had to be reduced since the hydraulic modeling of every day of the whole simulation period would have been very time-consuming.

Despite these simplifications the model accuracy is good. The validation of ecological models against expert-based PNV maps in areas where the actual vegetation cannot be used because of strong anthropogenic modification is common practice (Hickler et al., 2012; Somodi et al., 2017). We chose the fuzzy approach to assess the agreement because it allowed the consideration of similarities between the vegetation communities along the successional gradient from “initial phase” to the “terminal stage” and the consideration of spatial proximity between cells. It is therefore regarded closer to human judgment than the traditional binary methods for map comparison that only report correct/incorrect and do not distinguish small differences from large differences (Visser and De Nijs, 2006). Only the early succession phases (area < 5%) did not match well but are also the most difficult to model because of their short life span and high sensitivity to disturbances. It should be noted however that the expert-based estimation is highly uncertain too. Naturally occurring reeds for example are not easily distinguishable from anthropogenic reed occurrences. Their dominance and persistence in some areas can result from irregular mowing of former wetland meadows that allowed very competitive reed species like *Phragmites australis* to establish a dense cover and suppress the growth of trees and shrubs until today. Another complication is that *Salix alba* has been planted at some locations to cultivate cuttings for brush layering constructions.

Conclusion

With the help of a dynamic floodplain vegetation model accounting for the processes recruitment, and the morphologic and physiologic effect of floods on plant communities we were able to reconstruct the succession dynamics of a large European river that suffered drastic alterations of its site condition in high spatial and temporal resolution and were able to isolate the yearly flood duration as the main driving factor. Our results of special relevance because long-term observations of the development of the flood plain vegetation of large rivers are extremely rare and difficult to interpret because of the high degree of direct modification of the actual vegetation through agriculture and forestry. The good agreement of the model results with the PNV map shows that our approach is a good alternative to the traditional, expert-based method to create a benchmark map for floodplain conservation and restoration projects with the big advantage of being comprehensive and reproducible. Moreover, the dynamic nature of our modeling approach allows for detailed analyses of the development of vegetation patterns as well as projections under different environmental scenarios (e.g. climate change, environmental flow assessment) (Politti et al., 2014; Rivaes et al., 2014, 2015).

4.6 References

Aggenbach, C. J. S., & Pelsma, T. A. H. M. (2003). Hydro-ecological assessment of vegetation of Dutch river habitats. River Systems, 15(1–4), 199–210. https://doi.org/10.1127/lr/15/2003/199

Arco Aguilar, M.-J., González-González, R., Garzón-Machado, V., & Pizarro-Hernández, B. (2010). Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodiversity and Conservation, 19(11), 3089–3140. https://doi.org/10.1007/s10531-010-9881-2

Barnes, B. V, Pregitzer, K. S., Spies, T. A., & Spooner, V. H. (1982). Ecological forest site classification. Journal of Forestry, 80(8), 493–498.

Belz, J. U., & Frauenfelber-Kääb, R. (2007). Das Abflussregime des Rheins und seiner Nebenflüsse im 20. Jahrhundert: Analyse, Veränderungen, Trends. Internationale Kommission für die Hydrologie des Rheingebietes.

Bendix, J., & Hupp, C. R. (2000). Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes, 14(16–17), 2977–2990. https://doi.org/10.1002/1099-1085(200011/12)14:16/17<2977::AID-HYP130>3.0.CO;2-4

Benjankar, R., Egger, G., Jorde, K., Goodwin, P., & Glenn, N. F. (2011). Dynamic floodplain vegetation model development for the Kootenai River, USA. Journal of Environmental Management, 92(12), 3058–3070. https://doi.org/10.1016/j.jenvman.2011.07.017

Bernhardt, C. (2000). Die Rheinkorrektion. Der Bürger Im Staat, 50(2), 76–81.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., van Geest, G. J., Grift, R. E., … Roozen, F. C. J. M. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwater Biology, 47(4), 889–907. https://doi.org/10.1046/j.1365-2427.2002.00915.x

Buijse, A. D., Klijn, F., Leuven, R. S. E. W., Middelkoop, H., Schiemer, F., Thorp, J. H., & Wolfert, H. P. (2005). Rehabilitation of large rivers: references, achievements and integration into river management. Rivers, 15(1), 715–738. https://doi.org/10.1016/j.ecoleng.2012.02.005

Camporeale, C., & Ridolfi, L. (2006). Riparian vegetation distribution induced by river flow variability: A stochastic approach. Water Resources Research, 42(10), n/a-n/a. https://doi.org/10.1029/2006WR004933

Church, M. (1995). Geomorphic response to river flow regulation: Case studies and time-scales. Regulated Rivers: Research & Management, 11(1), 3–22. https://doi.org/10.1002/rrr.3450110103

Díaz-Redondo, M., Egger, G., Marchamalo, M., Damm, C., de Oliveira, R. P., & Schmitt, L. (2018). Targeting lateral connectivity and morphodynamics in a large river-floodplain system: The upper Rhine River. River Research and Applications, (April), 1–11. https://doi.org/10.1002/rra.3287

Diaz-Redondo, M., Egger, G., Marchamalo, M., Hohensinner, S., & Dister, E. (2017). Benchmarking Fluvial Dynamics for Process-Based River Restoration: the Upper Rhine River (1816–2014). River Research and Applications, 33(3), 403–414. https://doi.org/10.1002/rra.3077

Dister, E. (1980). Geobotanische Untersuchungen in der hessischen Rheinaue als Grundlage für die Naturschutzarbeit. Dissert. Univ. G/Sttingen, RFA.

Dister, E., Gomer, D., Obrdlik, P., Petermann, P., & Schneider, E. (1990). Water mangement and ecological perspectives of the upper rhine’s floodplains. Regulated Rivers: Research & Management, 5(1), 1–15. https://doi.org/10.1002/rrr.3450050102

Dynesius, M., & Nilsson, C. (1994). Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. Science, 266(5186), 753–762. https://doi.org/10.1126/science.266.5186.753

Egger, G., Politti, E., Garófano-Gómez, V., Blamauer, B., Ferreira, M. T., Rivaes, R., … Habersack, H. (2013). Embodying Interactions Between Riparian Vegetation and Fluvial Hydraulic Processes Within a Dynamic Floodplain Model: Concepts and Applications. In Ecohydraulics: An Integrated Approach (pp. 407–427). https://doi.org/10.1002/9781118526576.ch24

Florsheim, J. L., Mount, J. F., & Chin, A. (2008). Bank Erosion as a Desirable Attribute of Rivers. BioScience, 58(6), 519. https://doi.org/10.1641/B580608

Franz, E. H., & Bazzaz, F. a. (1977). Simulation of Vegetation Response to Modified Hydrologic Regimes: A Probabilistic Model Based on Niche Differentiation in a Floodplain Forest. Ecology, 58(1), 176–183. https://doi.org/10.2307/1935119

Friedman, J.M., & Lee, V. J. (2002). Extreme floods, channel change, and riparian forests along ephemeral streams. Ecological Monographs, 72(3), 409–425.

Friedman, Jonathan M., & Auble, G. T. (1999). Mortality of riparian box elder from sediment mobilization and extended inundation. Regulated Rivers: Research and Management, 15(5), 463–476. https://doi.org/10.1002/(SICI)1099-1646(199909/10)15:5<463::AID-RRR559>3.0.CO;2-Z

Gallusser, W. A., & Schenker, A. (1992). Die Auen am Oberrhein, Les zones alluviales du Rhin supérieur. Ausmaß und Perspektiven des Landschaftswandels am südlichen und mittleren Oberrhein seit 1800/Etendue et perspectives de l'évolution des paysages dans le secteur méridional et moyen du Rhin su. Springer.

García-Arias, A., & Francés, F. (2016). The RVDM: modelling impacts, evolution and competition processes to determine riparian vegetation dynamics. Ecohydrology, 9(3), 438–459. https://doi.org/10.1002/eco.1648

Glenz, C., Schlaepfer, R., Iorgulescu, I., & Kienast, F. (2006). Flooding tolerance of Central European tree and shrub species. Forest Ecology and Management, 235(1–3), 1–13. https://doi.org/10.1016/j.foreco.2006.05.065

Gumiero, B., Mant, J., Hein, T., Elso, J., & Boz, B. (2013). Linking the restoration of rivers and riparian zones/wetlands in Europe: Sharing knowledge through case studies. Ecological Engineering, 56, 36–50. https://doi.org/10.1016/j.ecoleng.2012.12.103

Gurnell, A. M. (2016). Hydrogeomorphology- Ecology Interactions in River Systems. River Research and Applications, 22(March 2014), 1085–1095. https://doi.org/10.1002/rra

Gurnell, A. M., & Petts, G. E. (2002). Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology, 47(4), 581–600. https://doi.org/10.1046/j.1365-2427.2002.00923.x

Habersack, H., & Piégay, H. (2007). 27 River restoration in the Alps and their surroundings: past experience and future challenges. Developments in Earth Surface Processes, 11(07), 703–735. https://doi.org/10.1016/S0928-2025(07)11161-5

Herget, J., & et al., et al. (2005). Engineering impacts on river channels in the River Rhine catchment. Erdkunde, 59(3/4), 294–319. https://doi.org/10.3112/erdkunde.2005.03.07

Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., … Sykes, M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography, 21(1), 50–63. https://doi.org/10.1111/j.1466-8238.2010.00613.x

Hohensinner, S., Habersack, H., Jungwirth, M., & Zauner, G. (2004). Reconstruction of the characteristics of a natural alluvial river-floodplain system and hydromorphological changes following human modifications: The Danube River (1812-1991). River Research and Applications, 20(1), 25–41. https://doi.org/10.1002/rra.719

Hohensinner, S., Jungwirth, M., Muhar, S., & Schmutz, S. (2014). Importance of multi-dimensional morphodynamics for habitat evolution: Danube River 1715-2006. Geomorphology, 215, 3–19. https://doi.org/10.1016/j.geomorph.2013.08.001

Horn, H. S. (1974). The Ecology of Secondary Succession. Annual Review of Ecology and Systematics, 5(1), 25–37. https://doi.org/10.1146/annurev.es.05.110174.000325

Jungwirth, M., Muhar, S., & Schmutz, S. (2002). Re-establishing and assessing ecological integrity in riverine landscapes. Freshwater Biology, 47(4), 867–887. https://doi.org/10.1046/j.1365-2427.2002.00914.x

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences, 106(1), 110–127.

Keane, R. E., Holsinger, L. M., Pratt, S. D., Robert, E., Lisa, M., & Simulating, S. D. (2006). Simulating Historical Landscape Dynamics Using the Landscape Fire Succession Model LANDSUM version 4 . 0. (April).

Kelly, A., Powell, D. C., & Riggs, R. a. (2005). Predicting Potential Natural Vegetation in an Interior Northwest Landscape Using Classification Tree Modeling and a GIS. Western Journal of Applied Forestry, 20(2), 117–127.

Kikyo, M., Tanaka, K., Kamei, T., Ozaki, K., Fujiwara, T., Inoue, E., … Takai, Y. (1999). An FH domain-containing Bnr1p is a multifunctional protein interacting with a variety of cytoskeletal proteins in Saccharomyces cerevisiae. Oncogene, 18(50), 7046–7054. https://doi.org/10.1038/sj.onc.1203184

Kovalchik, B. L., & Clausnitzer, R. R. (2001). Classification and Management of Aquatic , Riparian , and Wetland Sites on the National Forests of Eastern Washington : Series Description. Sites The Journal Of 20Th Century Contemporary French Studies, (September), 354.

Lai, Y. G. (2008). SRH-2D version 2: Theory and User's Manual. Sedimentation and River Hydraulics–Two-Dimensional River Flow Modeling, US Department of Interior, Bureau of Reclamation, November.

Lenders, H. J. R., Leuven, R. S. E. W., Nienhuis, P. H., de Nooij, R. J. W., & Van Rooij, S. A. M. (2001). BIO-SAFE: a method for evaluation of biodiversity values on the basis of political and legal criteria. Landscape and Urban Planning, 55(2), 121–137. https://doi.org/10.1016/S0169-2046(01)00149-9

Li, C. (2000). Reconstruction of natural fire regimes through ecological modelling. Ecological Modelling, 134(2–3), 129–144. https://doi.org/10.1016/S0304-3800(00)00290-8

Magilligan, F. J., & Nislow, K. H. (2005). Changes in hydrologic regime by dams. Geomorphology, 71(1–2), 61–78. https://doi.org/10.1016/j.geomorph.2004.08.017

Mahoney, J. M., & Rood, S. B. (1998). Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands, 18(4), 634–645.

Merritt, D. M., Scott, M. L., Leroy Poff, N., Auble, G. T., & Lytle, D. A. (2010). Theory, methods and tools for determining environmental flows for riparian vegetation: Riparian vegetation-flow response guilds. Freshwater Biology, 55(1), 206–225. https://doi.org/10.1111/j.1365-2427.2009.02206.x

Naiman, R. J., Decamps, H., & McClain, M. E. (2005). Riparia: ecology, conservation, and management of streamside communities. Elsevier, Academic Press.

Naiman, R. J., Latterell, J. J., Pettit, N. E., & Olden, J. D. (2008). Flow variability and the biophysical vitality of river systems. Comptes Rendus - Geoscience, 340(9–10), 629–643. https://doi.org/10.1016/j.crte.2008.01.002

Ollero, A. (2010). Channel changes and floodplain management in the meandering middle Ebro River, Spain. Geomorphology, 117(3–4), 247–260. https://doi.org/10.1016/j.geomorph.2009.01.015

Oorschot, M. van, Kleinhans, M., Geerling, G., & Middelkoop, H. (2016). Distinct patterns of interaction between vegetation and morphodynamics. Earth Surface Processes and Landforms, 41(6), 791–808. https://doi.org/10.1002/esp.3864

Petts, G. E., & Gurnell, A. M. (2005). Dams and geomorphology: Research progress and future directions. Geomorphology, 71(1–2), 27–47. https://doi.org/10.1016/j.geomorph.2004.02.015

Politti, E., Egger, G., Angermann, K., Rivaes, R., Blamauer, B., Klösch, M., … Habersack, H. (2014). Evaluating climate change impacts on Alpine floodplain vegetation. Hydrobiologia, 737(1), 225–243. https://doi.org/10.1007/s10750-013-1801-5

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., … Winterbourn, M. J. (1988). Patch Dynamics in Lotic Systems: The Stream as a Mosaic. Journal of the North American Benthological Society, 7(4), 503–524. https://doi.org/10.2307/1467303

Ricotta, C., Carranza, M. L., Avena, G., & Blasi, C. (2000). Quantitative comparison of the diversity of landscapes with actual vs. potential natural vegetation. Applied Vegetation Science, 3(2), 157–162. https://doi.org/10.2307/1478994

Rivaes, R., Rodríguez-González, P. M., Albuquerque, A., Pinheiro, A. N., Egger, G., & Ferreira, M. T. (2015). Reducing river regulation effects on riparian vegetation using flushing flow regimes. Ecological Engineering, 81, 428–438. https://doi.org/10.1016/j.ecoleng.2015.04.059

Rivaes, R., Rodríguez-González, P. M., Ferreira, M. T., Pinheiro, A. N., Politti, E., Egger, G., … Francés, F. (2014). Modeling the evolution of riparian woodlands facing climate change in three european rivers with contrasting flow regimes. PLoS ONE, 9(10). https://doi.org/10.1371/journal.pone.0110200

Rosati, L., Marignani, M., & Blasi, C. (2008). A gap analysis comparing Natura 2000 vs National Protected Area network with potential natural vegetation. Community Ecology, 9(2), 147–154. https://doi.org/10.1556/ComEc.9.2008.2.3

Runhaar, J. (2003). Natuurgericht landevaluatiesysteem (NATLES) versie 2. Alterra-rapport;550. Retrieved from http://library.wur.nl/wasp/bestanden/LUWPUBRD_00321225_A502_001.pdf

Saxton, K. E., Rawls, W. J., Romberger, J. S., & Papendick, R. I. (1986). Estimating Generalized Soil-water Characteristics from Texture. Soil Science Society of America Journal, 50(4), 1031. https://doi.org/10.2136/sssaj1986.03615995005000040039x

Somodi, I., Molnár, Z., Czúcz, B., Bede-Fazekas, Á., Bölöni, J., Pásztor, L., … Zimmermann, N. E. (2017). Implementation and application of multiple potential natural vegetation models – a case study of Hungary. Journal of Vegetation Science, 28(6), 1260–1269. https://doi.org/10.1111/jvs.12564

Stanford, J. A., Lorang, M. S., & Hauer, F. R. (2005). The shifting habitat mosaic of river ecosystems. SIL Proceedings, 1922-2010, 29(1), 123–136. https://doi.org/10.1080/03680770.2005.11901979

Swetnam, T. W., Allen, C. D., & Betancourt, J. L. (1999). Applied Historical Ecology: Using the Past To Manage for the Future. Ecological Applications, 9(4), 1189–1206. https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2

Taylor, A. R., Chen, H. Y. H., & VanDamme, L. (2009). A review of forest succession models and their suitability for forest management planning. Forest Science, 55(1), 23–36.

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. Environmental Conservation, 29(3), 308–330. https://doi.org/10.1017/S037689290200022X

Tockner, K., Uehlinger, U., & Robinson, C. T. (2009). Rivers of Europe. Academic Press.

van Vliet, J., Hagen-Zanker, A., Hurkens, J., & van Delden, H. (2013). A fuzzy set approach to assess the predictive accuracy of land use simulations. Ecological Modelling, 261–262, 32–42. https://doi.org/10.1016/j.ecolmodel.2013.03.019

Vaughan, I. P., Diamond, M., Gurnell, A. M., Hall, K. A., Jenkins, A., Milner, N. J., … Ormerod, S. J. (2009). Integrating ecology with hydromorphology: A priority for river science and management. Aquatic Conservation: Marine and Freshwater Ecosystems, 19(1), 113–125. https://doi.org/10.1002/aqc.895

Visser, H., & De Nijs, T. (2006). The map comparison kit. Environmental Modelling and Software, 21(3), 346–358. https://doi.org/10.1016/j.envsoft.2004.11.013

Ward, J. V., & Stanford, J. A. (1995). Ecosystems and Its Disruption By Flow Regulation. Regulated Rivers: Research & Management, II(July 1994), 105–119. https://doi.org/10.1002/rrr.3450110109

Ward, J. V., Tockner, K., & Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research & Management, 15(1–3), 125–139. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E

Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S., & Stanford, J. A. (2007). Climate, hydrologic disturbance, and succession: Drivers of floodplain pattern. Ecology, 88(4), 940–953. https://doi.org/10.1890/05-1149

Wimberly, M. C. (2002). Spatial simulation of historical landscape patterns in coastal forests of the Pacific Northwest. Canadian Journal of Forest Research, 32(8), 1316–1328. https://doi.org/10.1139/x02-054

5 THE POTENTIAL NATURAL VEGETATION OF LARGE RIVER FLOODPLAINS – FROM DYNAMIC TO STATIC EQUILIBRIUM

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5.1 Abstract

The potential natural vegetation (PNV) is a useful benchmark for the restoration of large river floodplains because very few natural reference reaches exist. Expert-based approaches and different types of ecological models (static and dynamic) are commonly used for its estimation despite the conceptual differences they imply. For natural floodplains a static concept of PNV is not reasonable, as natural disturbances cause a constant resetting of succession. However, various forms of river regulation have disrupted the natural dynamics of most large European rivers for centuries. Therefore, we asked whether the consideration of succession dynamics and time-dependent habitat turnover are still relevant factors for PNV reconstruction.

To answer this we compared the results of a simulation of the vegetation succession (1872 to 2016) of a segment of the upper Rhine river after regulation (damming, straightening and bank protection) to different statistic and expert-based modeling approaches for the reconstruction of the PNV. The validation of the different PNV estimation methods against a set of independent reference plots and the direct comparison of their results revealed very similar performances. We therefore conclude that due to a lack of large disturbances, the vegetation of regulated large rivers has reached a near-equilibrium state with the altered hydrologic regime and that a static perception of its PNV may be justified. Consequently, statistical models seem to be the best option for its reconstruction since they need relatively few resources (data, time, expert knowledge) and are reproducible.

Keywords: potential natural vegetation, PNV, riparian vegetation, floodplain, modeling, large rivers

5.2 Introduction

River floodplains are amongst the most species-rich and productive ecosystems (Naiman and Decamps, 1997). At the same time, these ecosystems are one of the most threatened and modified worldwide (Tockner and Stanford, 2002), highlighting the need for conservation and restoration efforts (Myers et al., 2000; Buijse et al., 2002). Such efforts, however, are challenged by a lack of natural reference sites for orientation (Whited et al., 2007). Indeed, 90% of river floodplains in Europe and North America are used for agriculture or forestry and no longer harbor natural vegetation communities (Tockner and Stanford, 2002). Where no natural references exist, a potential natural vegetation (PNV) is often reconstructed and used as benchmark (Carranza et al., 2003; Klimas et al., 2009; Hickler et al., 2012; Schleupner and Schneider, 2013; Shi et al., 2016; Justice et al., 2017).

But the concept of PNV and the methods for its reconstruction are highly controversial (Chiarucci et al., 2010; Mucina, 2010; Loidi and Fernández-González, 2012; Somodi et al., 2012). PNV was first defined by Tüxen (1956) as the vegetation that would develop under present site conditions if human influences were excluded completely, and succession would reach its climax stage at once. It has often been thought of as a historic, pre-human reference condition (Hall and McGlone, 2006; Willis and Birks, 2006). However this idea has provoked disagreement (Mitchell, 2005; Carrión and Fernández, 2009) because it ignores that environmental conditions have changed since pre-human times (Nilsson et al., 2005; Dotterweich, 2008). Therefore, it has been argued that an estimation of the natural vegetation based on the assessment of present-day natural vegetation remnants is more reliable (Kowarik, 1987). But in areas with historically high levels of land use transformation this assessment is also prone to uncertainties (Zerbe, 1998). Another much-discussed issue is the consideration of ecosystem dynamics and stochasticity (Härdtle, 1995; Chiarucci et al., 2010), which are especially relevant in naturally disturbed areas (Leuschner, 1997; Zerbe, 1998; Jackson, 2013). The traditional PNV estimation method is expert-based and follows a floristic-sociological approach (Westhoff and Van Der Maarel, 1978). It relies on the fieldworker's assessment and understanding of ecology to extrapolate present-day natural vegetation remnants to similar environments (Kowarik, 1987; Moravec, 1998). This approach, however, lacks transparency and reproducibility. Furthermore, its implied static perception of PNV makes predictions in dynamic systems questionable (Mucina, 2010). More comprehensive and also widely used for PNV estimations are ecological models based on the relationship between vegetation and environmental variables (Zerbe, 1998; Somodi et al., 2012). Two types can be differentiated that imply fundamental conceptual differences: static models and dynamic models (Hannon and Ruth, 1998). Static models describe a phenomenon at a given point in time and assume equilibrium between the vegetation and its environment. Dynamic models (e.g. process-based models or mechanistic models) are based on ecological processes and differ from static models by explicitly incorporating time-dependent changes in the system state. Therefore they are able to capture the transient response of vegetation to a changing environment (Hannon and Ruth, 2014).

Little attention, however, has been given to issues surrounding PNV in fluvial contexts. The first modeling approaches of PNV in floodplains were static and tried to explain the vegetation patterns along vertical (height above channel) and lateral (distance away from channel) gradients (Hosner and Minckler, 1963; Nixon et al., 1977; Robertson et al., 1978; Hughes, 1988; Bowman and Mcdonough, 1991; Glavac et al., 1992; Ward and Stanford, 1995; Ellenberg, 1996; Roberts and Ludwig, 2016). Later more advanced static models emerged that relate the vegetation distribution to a set of hydrologic variables based on expert rules (Pieterse et al., 1998; Lenders et al., 2001; Jungwirth et al., 2002; Aggenbach and Pelsma, 2003; Runhaar, 2003; Baptist et al., 2004; Fuchs et al., 2012) or statistical analyses (Franz and Bazzaz, 1977; Auble et al., 1994; Menuz, 2011). Dynamic floodplain vegetation models combine a simulation of the hydrodynamics with the modeling of ecological processes (e.g. growth and mortality, recruitment, succession/retrogression, competition) and are used to describe the vegetation development over time (Pearlstine et al., 1985; Camporeale and Ridolfi, 2006; Benjankar et al., 2011; García-Arias and Francés, 2016). More recently, the dynamic feedbacks between vegetation and hydro-geomorphological processes have also been incorporated (Camporeale et al., 2013; Oorschot et al., 2016). We argue that for floodplains of unregulated rivers the original static concept of PNV based on a climax stage of vegetation is not reasonable because successional sequences are repeatedly rejuvenated and reset by hydro-geomorphological disturbances (Pringle et al., 1988). It has been theorized that at the appropriate scale the proportion of successional phases would remain constant when processes of regression are compensated by progression, a dynamic equilibrium referred to as shifting steady-state mosaic (Bormann and Likens, 1979; Stanford et al., 2005; Geerling et al., 2006). While methodological advances reflect the growing recognition in the importance of allowing dynamic change in PNV estimation, various forms of river regulation have disrupted the natural dynamics in most large rivers (Dynesius and Nilsson, 1994; Buijse et al., 2002). River damming and bank stabilization are the main reason for the impediment of dynamic geomorphological processes (e.g. avulsion, meandering, braiding) and decrease of hydrodynamic variability and disturbance in the riparian zone (Church, 1995; Nilsson and Berggren, 2000; Magilligan and Nislow, 2005; Petts and Gurnell, 2005).

In this context, we investigated whether the consideration of succession dynamics and habitat turnover are still relevant factors for the model-based reconstruction of the PNV of regulated large river floodplains. Our hypothesis is that they can be neglected because riparian vegetation of regulated large rivers has reached a stable equilibrium due to the loss of natural disturbance dynamics. To test this idea we compared the results of a simulation of the succession dynamics (1872 to 2016) of the floodplain vegetation of a segment of the heavily regulated upper Rhine River to different static approaches for the estimation of its PNV a) a statistical model based on hydrologic predictors and the geomorphological age of site b) a statistical model only based on hydrologic predictors and c) a gradient approach only based on the distance to the mean water level.

5.3 Methodology

5.3.1 Study Area

The Rhine River is one of the largest rivers in Central Europe, with a length of approximately 1230 km and a catchment area of approximately 185300 km^2. Our study area lies in the Upper Rhine region where the nival discharge regime is strongly influenced by snow-melt in the Alps (Belz and Frauenfelber-Kääb, 2007). Until the beginning of the 19th century the Upper Rhine could still be considered in natural condition (Gallusser and Schenker, 1992) and was classified as a highly dynamic, island-dominated, anabranching river system (Gurnell and Petts, 2002; Herget and et al., 2005). During the course of the 19th century, however, the Upper Rhine River was transformed into a single-thread channel by cutting off meander bends and building groins and bank revetments (Bernhardt, 2000). In the 20th century river regulation intensified through the construction of 10 hydropower plants in the main channel or in artificial side channels (Dister et al., 1990). During this time industry and settlements also expanded in the study area (Habersack and Piégay, 2007). The study area is the “Raststatter Rheinaue”, a nature reserve on the eastern, German side of the floodplain that includes a 9-km segment of the Upper Rhine River downstream from the Iffezheim dam to the confluence of the river Murg (Rhine km 335.8 – 345, 114–110 m a.s.l.). It is only limited by flood dykes towards the east and is still regularly flooded. The study area covers approximately 645 ha (including water bodies).

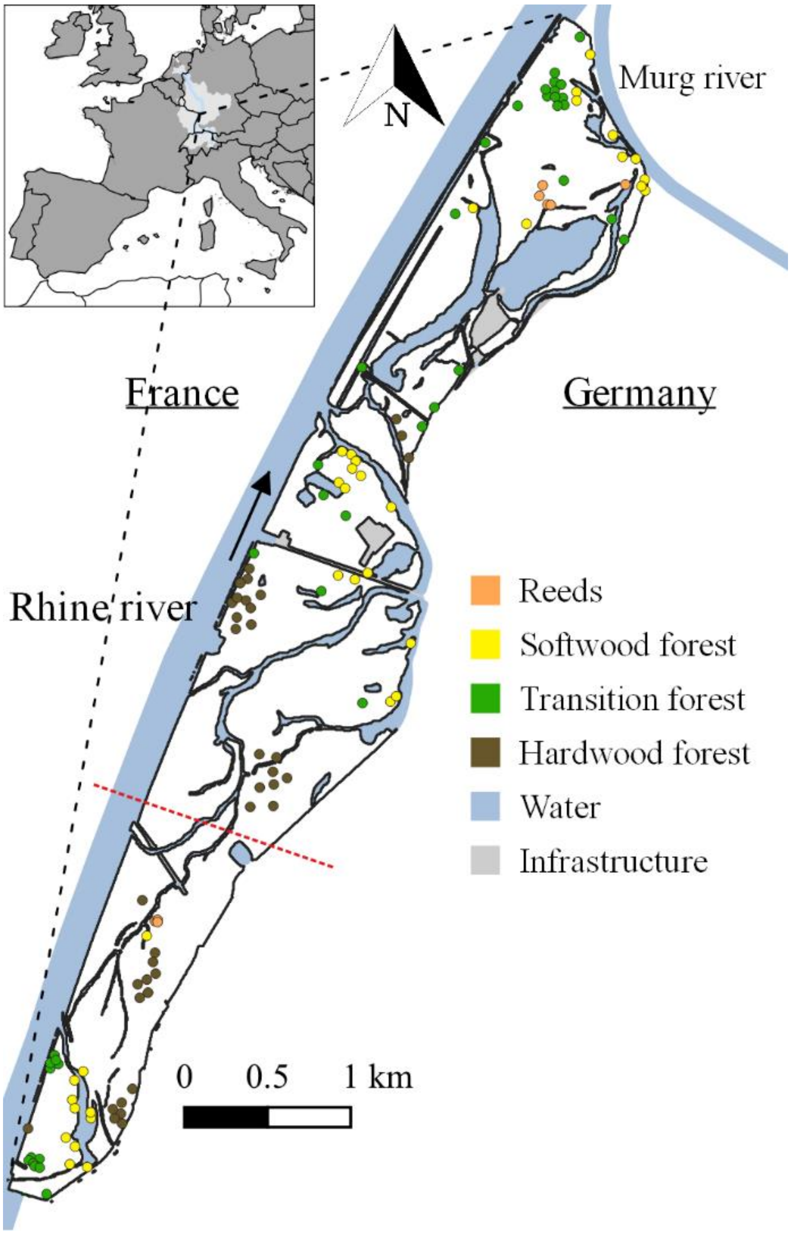

Figure 18: Upper left corner: Location of study area in central Europe (dark grey) and the Rhine basin (light grey); Rest: Location of the study area along the eastern (German) side of the Rhine river and reference PNV plots, the dashed red line indicate the separation in calibration (downstream) and validation data (upstream)

5.3.2 Material and Data

Historic maps

Because the Upper Rhine has been the border between France and Germany, detailed maps were produced for the planning of the river straightening in the beginning of the 19th century. These indicate the location of water bodies, islands and gravel/sand bars within the aquatic area, as well as land uses in the floodplain (grasslands, forests, croplands and settlements). Our work is based primarily on four historical maps from that time (1816, 1838, 1852, 1872) that were georeferenced and classified in natural (natural water body, gravel/sand bar, grassland and forest) or anthropic (artificial water body, cropland, settlement and industry) habitat categories (for details see: Diaz-Redondo et al., 2017).

Discharge data and Hydrodynamic model

The analysis of the flow regime of the study area for the whole simulation period is based on the Maxau gauging station (Rhine km 362.3) which has the longest continuous record of daily discharge (1921 – today) and also records of the annual low, mean and high discharges for the period 1872 -1921 (Diaz-Redondo et al., 2017). A two-dimensional hydrodynamic model (SRH-2D; Lai, 2008) of the Rhine river and its eastern floodplain was set up. The model bathymetry is based on a high-resolution (1 m) DEM (Wasserstrassen- und Schifffahrtsverwaltung des Bundes (WSV), 2016) supplemented by longitudinal profiles and cross-sections through the main water bodies in the study area (Díaz-Redondo et al., 2018). The model mesh consists of 149900 nodes with an average distance of 20 m in the main channel, 10 m in the floodplain and down to 2 m in the river bank and dam zones. Break lines were integrated manually. Water surface elevations (WSE) for 6 flood events with return periods between 1 and 100 years provided by the German Federal Agency for Hydrology (BfG) were used for model calibration and setting of the lower boundary condition. Manning roughness coefficients were first appointed to the model elements based on different land use and lie around 0.083 for the floodplain forest and around 0.026 for the side channels and 0.037 for the main river channel.

Calibration was performed by adjusting Manning's roughness coefficients to minimize the difference between modelled and measured WSEs. Mean WSE errors were between 1 cm for flood events with short return periods and 20 cm for higher return periods.

Calibration and validation data

We used an expert-based PNV map (Ochs et al., 2019) and analyzed the historical land-use to delineate likely reference areas for four main vegetation types: Reeds, softwood forest, transition forest and hardwood. Within these areas a total of 130 random sampling plots (radius = 5 m) were distributed with a minimum distance between them of 50 m. The PNV-type of the plots was verified during several field visits (Föll and Egger, 2017). The verification was guided by indicator species from the herb and shrub layers (see Table B 1). Reeds could be confirmed in 8 plots, softwood forest in 36 plots, transition forest in 40 plots and 37 plots could be clearly identified as hardwood forest. To increase the independency of the assessment of the predictive performance and comparison between the different modeling approaches we split the study area geographically perpendicular to the river axis (Wenger and Olden, 2012). The downstream part that represents between 30% and 40 % of the reference plots of each vegetation type was used for validation (Figure 18).

5.3.3 Dynamic succession model (DM)

The dynamic floodplain vegetation model CASIMIR (Benjankar et al., 2011; Egger et al., 2013) was used to predict the PNV by simulating the succession of the floodplain vegetation from 1872 to 2016. The time period was chosen because by 1872 the study area had already suffered the main hydro-morphological impacts through river straightening and channelization (Bernhardt, 2000). In the model, the riparian vegetation is represented in succession lines and their respective succession phases (Table A 2). The dynamic modules are: Recruitment, controlled by the spring mean water level as described by the recruitment box model (Mahoney and Rood, 1998) and Succession (Progression/Retrogression), controlled by the disturbance indicators "flood duration" and "shear stress" (Formann et al., 2014). Each year the recruitment module checks for bare soils in the bank and floodplain zone as well as the water levels that allow seedling survival (Table A 3) and the disturbance module checks whether the critical values of the disturbance indicators are surpassed (Table A 4 and Table A 5). The result of one simulated year will be used as input for the next year. The parametrization of the model was based on analyses of historic maps and historic discharge data. The model was calibrated against an expert-based PNV estimation of the upstream part of the study area so that the reference plots for validation can also be considered independent (for a detailed description of the model functioning and calibration/validation see Ochs et al., 2019 as well as Appendix B and C).

For comparability the succession phases of the final year were aggregated to match the main PNV types in the study area (Table B 1).

5.3.4 Statistic Models (SM1 and SM2)

The statistic modeling approach for the classification of the main PNV types was based on the random forest algorithm (Breiman, 2001). Random forest selects random bootstrap samples from a given dataset to build a set of decision trees. The final prediction is based on the majority vote from the individually developed trees.

We chose three predictors representing the hydrological control factors of riparian vegetation: flood duration, water depth and shear stress. For the flood duration raster, the average flood duration of each grid cell during the growing periods between 1921 -2016 was calculated (see Appendix B). Maps of water depth and shear stress were calculated for HQ10 (4100 m^3/s) so that the whole floodplain could be represented. In addition, we tested the influence of habitat age. The geomorphological age of different areas of the floodplain was derived through the analyses of the changes from water surfaces to sand and gravel bars on historic maps (Diaz-Redondo et al., 2017).

We built two different models: SM1 was based on the hydrological predictors and geomorphological age, SM2 considered only the hydrological predictors. The models were set to grow 1000 trees based on bootstrap samples from the calibration plots. The sample was balanced to compensate for the overrepresentation of softwood forest in the reference plots which according to an expert-based PNV map of 2017 covered around 10% of the study area. The statistical modeling was done in the R environment using the "randomForest" package (Liaw and Wiener, 2002).

5.3.5 Gradient model (GM)

The German Federal Institute of Hydrology (BfG) developed a gradient model for the large-scale assessment of the main floodplain vegetation types for the free-flowing parts of River Rhine and Elbe in Germany. It is based on the field-observation that the occurrence of Salix alba at a site correlates with the relative height to the mean water level and the mean annual flood duration (Schleuter, 2014). The mean annual flood duration of a grid cell is calculated as follows (Schleuter, 2016):

$$F = -70.599 * \ Ln(X + 0.50) + 88.711$$

F = mean annual flood duration

X = relative height to mean water level (m)

The PNV types are then assigned based on expert knowledge (Table 6).

PNV-type	Relative height to mean water level (m)	Mean annual flood duration
Reeds, annuals	< -0.14	220 – 160
Softwood forest	-0.14 – 0.63	160 – 80
Transition forest	0.63 – 1.23	80 – 50
Hardwood forest	1.23 >	50 – 0

Table 6: Main PNV-types, relative height to the mean water level and mean annual flood duration according to the GM (Schleuter, 2016)

5.3.6 Model validation and comparison

For validation of the predictive performance all models were tested against the same set of geographically separated reference plots. Based on a confusion matrix we calculated the global metrics overall accuracy (OA) and kappa coefficient (K) (Cohen, 1960), which corrects the OA for chance agreement. In addition, we calculated Sensitivity and Specificity for each PNV class. For comparison between the models all area-wide predictions were directly compared to each other by calculating the metrics Kappa (K), Kappa Location (KLoc) and Kappa histogram (Khist). KLoc describes the similarity of spatial allocation of categories of the two compared maps, and Khist describes the quantitative similarity (Pontius, 2000). The following rating system was applied: values greater than 0.75 indicate very good-to-excellent agreement, values between 0.40 and 0.75 indicate fair-to-good agreement, and values of 0.40 or less indicate poor agreement (Landis and Koch, 1977).

5.3.7 Results

The results of the different approaches to reconstruct the PNV of our study area are shown in Figure 19. The overall agreement between the models was good. All approaches predicted hardwood forests to be the dominant vegetation class followed by transition forests, softwood forests and reeds (Table 7). Along the same sequence the agreement of the predictions between the approaches diminished (Table 8). Hardwood forests were predicted for about 50% of the study area by all models and the agreement (spatial and quantitative) was excellent to very good. Transition forests were estimated to cover around 35% by DM, SM1 and SM2 but only 26% by GM. The similarity of the predictions of DM and SM1/2 was very good but only fair when compared to GM. Softwood forests were predicted on only 7% of the area by the DM but nearly twice as much by the other models. The agreement between the DM and SM1/2 still can be considered fair but showed high discrepancies to GM. Reeds presented poor agreement between all models, especially spatially.

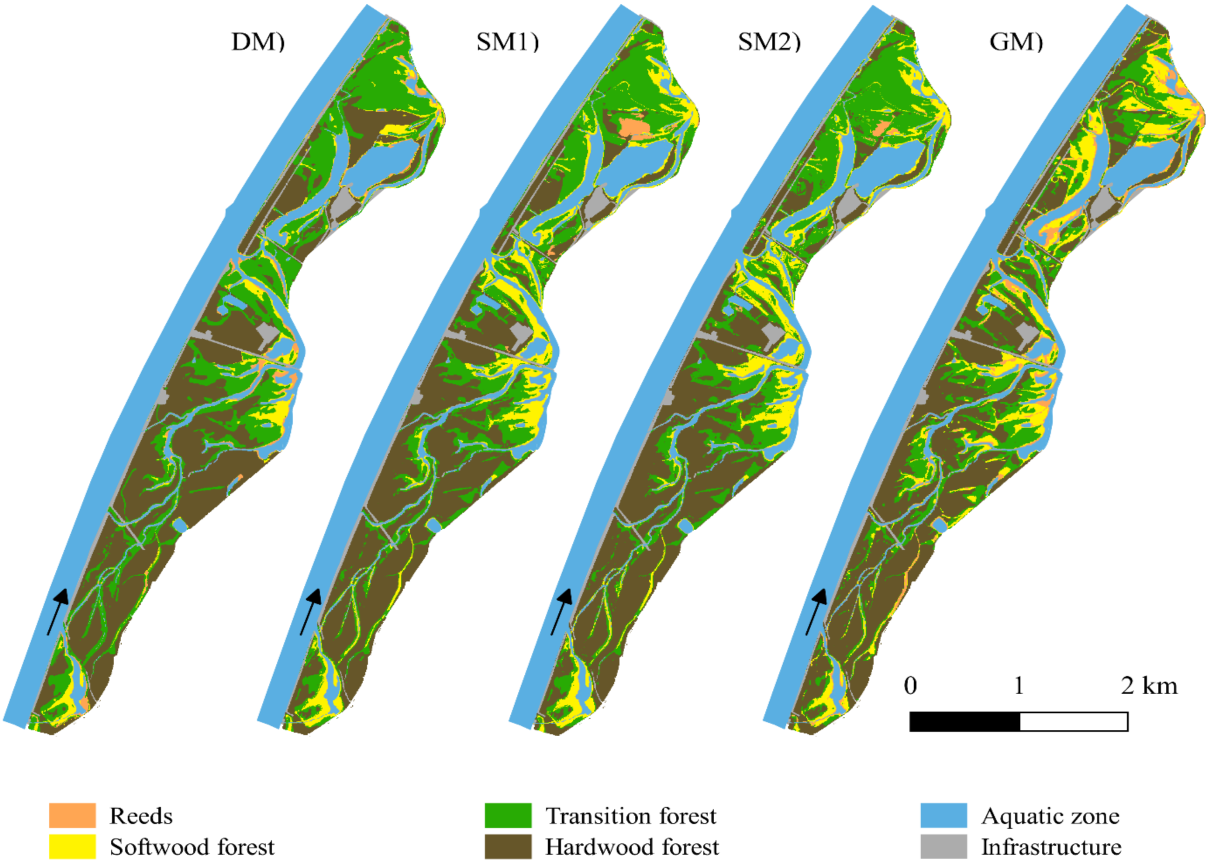

Figure 19: Predicted distribution of PNV types by the 4 modeling approaches

		DM	SM1	SM2	GM
Reeds	Area (ha)	17.15	12.93	15.12	28.09
	Area (%)	3.5	2.6	3	5.7
Softwood forest	Area (ha)	32.19	70.75	70.40	78.67
	Area (%)	6.5	14.37	14.2	15.9
Transition forest	Area (ha)	183.25	164.28	161.34	129.29
	Area (%)	36.9	33.3	32.6	26.1
Hardwood forest	Area (ha)	263.43	247.75	248.85	259.93
	Area (%)	53.1	50.0	50.2	52.4

Table 7: Total areas of the PNV types predicted by the 4 modeling approaches

	SM1			SM2			GM		
	K	Kloc	Khist	K	Kloc	Khist	K	Kloc	Khist
DM	0.59	0.68	0.87	0.53	0.60	0.87	0.42	0.52	0.81
Reeds	0.01	0.10	0.86	0.10	0.10	0.93	0.36	0.48	0.54
Softwood forests	0.43	0.74	0.59	0.44	0.74	0.60	0.25	0.46	0.54
Transition forests	0.55	0.60	0.92	0.46	0.51	0.72	0.30	0.40	0.75
Hardwood forests	0.74	0.79	0.94	0.68	0.72	0.94	0.60	0.61	0.99
SM1				0.87	0.88	0.98	0.51	0.58	0.88
Reeds				0.72	0.79	0.92	0.14	0.235	0.61
Softwood forests				0.96	0.96	0.99	0.44	0.43	0.92
Transition forests				0.83	0.84	0.99	0.42	0.50	0.83
Hardwood forests				0.89	0.89	0.99	0.71	0.74	0.95
SM2							0.51	0.56	0.89
Reeds							0.16	0.23	0.68
Softwood forests							0.41	0.44	0.93
Transition forests							0.42	0.50	0.85
Hardwood forests							0.70	0.72	0.95

Table 8: Agreement metrics between the four modelling approaches (green = good-to-excellent; yellow = fair-to-good; grey = poor)

Validation

Overall the DM, SM1 and SM2 showed good and the GM fair predictive performance. Notably, SM1 and SM2 performed identically. All models were unable to detect reeds (sensitivity = 0). Softwood forest and Hardwood forests were predicted with very good accuracy. But SM1, SM2 and GM only identified around 50% of transition forest reference plots correctly.

The “Mean Decrease Accuracy” and “Mean Decrease Gini” measures of the random forest models both revealed flood duration to be the most important predictor. “Habitat age” and “shear stress” were the least important ones.

		DM	SM1	SM2	GM
	OA	0.80	0.76	0.76	0.69
	Kappa	0.72	0.65	0.65	0.54
Reeds	Sensitivity	0	0	0	0
	Specificity	0.97	1	1	0.97
Softwood forest	Sensitivity	0.72	0.90	0.90	0.72
	Specificity	1	0.90	0.90	1
Transition forest	Sensitivity	0.85	0.54	0.54	0.46
	Specificity	0.90	0.97	0.97	0.96
Hardwood forest	Sensitivity	1	1	1	1
	Specificity	0.85	0.77	0.77	0.59

Table 9: Accuracy measures of the four modelling approaches ((green = good-to-excellent; yellow = fair-to-good; grey = poor)

5.4 Discussion

The equally good performances of the dynamic and static modeling approaches in predicting the PNV of our study area support the hypothesis that due to the loss of natural disturbance dynamics the riparian vegetation in our study area has reached a stable equilibrium with the hydrological control factors.

Sensitivity analyses of the statistic model and the DM (Ochs et al., 2019) revealed that the PNV is mainly determined by "flood duration". But we show that the resulting pattern of softwood, transition and hardwood forest is explained equally well by a static average as a reconstruction of the temporal dynamics of the flood regime (DM). Even more, the fair results of the gradient approach show that the relative height to the mean water level also captures most of the influencing factors of riparian vegetation. With the predictor "habitat age", we wanted to include a time dimension to the static modeling approach as an indication of a possible successional progression. However, roughly 150 years after geomorphological changes have been impeded habitat age proved to have no influence on the present vegetation communities. The transition of the large-scale dynamic equilibrium of natural floodplain ecosystem to a more mature and stable state after river regulation has also been recognized by other studies (Tockner and Stanford, 2002; Hohensinner et al., 2004; Ollero, 2010; Diaz-Redondo et al., 2017) and has been mainly attributed to an impediment of morphologic dynamics through bank stabilization and flow regulation (Florsheim et al., 2008; Hohensinner et al., 2014).

To allow for the comparison of the model predictions we validated the results against a geographically separated holdout sample. The spatial blocking strategy increases the independency of the sample and allows an effective test of a models transferability (Wenger and Olden, 2012; Roberts et al., 2017). It meant however, a trade-off with the sample size used for calibration of the statistical model which already had to be considered small (Wisz et al., 2008). Nevertheless, random forests are recognized as one of the most accurate species distribution modeling techniques (Elith et al., 2006; Cutler et al., 2007). Also, some confidence about our results can be drawn from the good agreement between the modeling approaches themselves. The reference plots were identified based on indicator species from the herb and shrub layers (Table B 1) that usually develop without direct human manipulation (Metzger and Schultz, 1984; Gilliam, 2007). As opposed to area-wide expert-based assessments of PNV that are often used to validate ecological models in areas of high anthropogenic transformation (Hickler et al., 2012; Somodi et al., 2017) the reference plots are not extrapolated and therefore more comprehensive and less prone to uncertainties.

All tested modeling approaches simplify the complex floodplain ecosystem and are based on several assumptions. They assume that in our study area the hydrological control factors are most relevant and neglect other factors that are known to influence plant communities in floodplains. Regarding the occurrence of reeds this seems to be an oversimplification since no model was able to detect it. The proliferation and dominance of *Phragmites australis* can be linked to nutrient competition and allelopathy (Hazelton et al., 2014; Uddin and Robinson, 2018). The fixed topographic input and disregard of the complex hydro-morphological processes normally occurring within the floodplain (Gurnell, 2016) can be justified in part by river regulation measures and artificially stabilized banks (a further in-depth discussion of the uncertainties regarding the dynamic model Casimir vegetation can be found here: Benjankar et al., 2011 and Ochs et al., 2019). Another obvious source of prediction bias for both the statistic and dynamic model are possible errors in the hydrological model and the historic maps that were used for parameterization.

In addition to the predictive performance, other important criteria when choosing a model are the required resources and deployment time. The simulation of succession dynamics for nearly 150 years was only possible with access to data of high spatiotemporal resolution and a high level of expert knowledge as well as a laborious calibration process. The static models on the other hand needed less data, know-how and time. Especially the very simple gradient model (GM) which still showed fair agreement with the other modeling approaches doesn’t even need hydraulic simulations since it is only based on the relative distance to the mean water level.

Conclusion

The high degree of transformation of large river floodplains through forestry and agriculture makes PNV a valuable concept, particularly as a benchmark for conservation measures. Although the conceptual and methodological issues around PNV are much discussed (Chiarucci et al., 2010; Loidi and Fernández-González, 2012; Somodi et al., 2012) the specific challenges for its reconstruction in river flood plains have gained little attention. Because natural floodplains are a disturbance-driven ecosystem, the classical, static PNV definition is not reasonable. However, through the direct comparison of process-based and statistic modeling approaches for PNV we showed that after 150 years of river regulation and impediment of geomorphological dynamics the riparian vegetation has reached a stable equilibrium state with its hydrologic control factors. A static perception of its PNV seems justified. Consequently, statistical models are the best option for its reconstruction, since they need relatively few resources (data, time, expert knowledge) and are reproducible.

5.5 References

Aggenbach, C. J. S., & Pelsma, T. A. H. M. (2003). Hydro-ecological assessment of vegetation of Dutch river habitats. River Systems, 15(1–4), 199–210. https://doi.org/10.1127/lr/15/2003/199

Auble, G. T., Friedman, J. M., & Scott, M. L. (1994). Relating Riparian Vegetation to Present and Future Streamflows. Ecological Applications, 4(3), 544–554. https://doi.org/10.2307/1941956

Baptist, M. J., Penning, W. E., Duel, H., Smits, A. J. M., Geerling, G. W., Van der Lee, G. E. M., & Van Alphen, J. S. L. (2004). Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Research and Applications, 20(3), 285–297. https://doi.org/10.1002/rra.778

Belz, J. U., & Frauenfelber-Kääb, R. (2007). Das Abflussregime des Rheins und seiner Nebenflüsse im 20. Jahrhundert: Analyse, Veränderungen, Trends. Internationale Kommission für die Hydrologie des Rheingebietes.

Benjankar, R., Egger, G., Jorde, K., Goodwin, P., & Glenn, N. F. (2011). Dynamic floodplain vegetation model development for the Kootenai River, USA. Journal of Environmental Management, 92(12), 3058–3070. https://doi.org/10.1016/j.jenvman.2011.07.017

Bernhardt, C. (2000). Die Rheinkorrektion. Der Bürger Im Staat, 50(2), 76–81.

Bormann, F. H., & Likens, G. E. (1979). Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard Brook ecosystem study. Springer Science & Business Media.

Bowman, D. M. J. S., & Mcdonough, L. (1991). Tree Species Distribution across a Seasonally Flooded Elevation Gradient in the Australian Monsoon Tropics. Journal of Biogeography, 18(2), 203–212. https://doi.org/Doi 10.2307/2845293

Breiman, L. (2001). Random forests. Mach Learn, 45(1), 5–32. https://doi.org/10.1023/A:1010933404324

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., van Geest, G. J., Grift, R. E., … Roozen, F. C. J. M. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwater Biology, 47(4), 889–907. https://doi.org/10.1046/j.1365-2427.2002.00915.x

Camporeale, C., Perucca, E., Ridolfi, L., & Gurnell, A. M. (2013). MODELING THE INTERACTIONS BETWEEN RIVER MORPHODYNAMICS AND RIPARIAN VEGETATION. Reviews of Geophysics, 51(3), 379–414. https://doi.org/10.1002/rog.20014

Camporeale, C., & Ridolfi, L. (2006). Riparian vegetation distribution induced by river flow variability: A stochastic approach. Water Resources Research, 42(10), n/a-n/a. https://doi.org/10.1029/2006WR004933

Carranza, M. L., Ricotta, C., Fortini, P., & Blasi, C. (2003). Quantifying landscape change with actual vs. potential natural vegetation maps. Phytocoenologia, 33(4), 591–601. https://doi.org/10.1127/0340-269X/2003/0033-0591

Carrión, J. S., & Fernández, S. (2009). The survival of the “natural potential vegetation” concept (or the power of tradition): COMMENTARY. Journal of Biogeography, 36(12), 2202–2203. https://doi.org/10.1111/j.1365-2699.2009.02209.x

Chiarucci, A., Araújo, M. B., Decocq, G., Beierkuhnlein, C., & Fernández-Palacios, J. M. (2010). The concept of potential natural vegetation: An epitaph? Journal of Vegetation Science, 21(6), 1172–1178. https://doi.org/10.1111/j.1654-1103.2010.01218.x

Church, M. (1995). Geomorphic response to river flow regulation: Case studies and time-scales. Regulated Rivers: Research & Management, 11(1), 3–22. https://doi.org/10.1002/rrr.3450110103

Cohen, J. (1960). A Coefficient of Agreement for Nominal Scales. Educational and Psychological Measurement, 20(1), 37–46. https://doi.org/10.1177/001316446002000104

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random Forests for Classification in Ecology. Ecology, 88(11), 2783–2792. https://doi.org/10.1890/07-0539.1

Díaz-Redondo, M., Egger, G., Marchamalo, M., Damm, C., de Oliveira, R. P., & Schmitt, L. (2018). Targeting lateral connectivity and morphodynamics in a large river-floodplain system:

The upper Rhine River. River Research and Applications, (April), 1–11. https://doi.org/10.1002/rra.3287

Diaz-Redondo, M., Egger, G., Marchamalo, M., Hohensinner, S., & Dister, E. (2017). Benchmarking Fluvial Dynamics for Process-Based River Restoration: the Upper Rhine River (1816–2014). River Research and Applications, 33(3), 403–414. https://doi.org/10.1002/rra.3077

Dister, E., Gomer, D., Obrdlik, P., Petermann, P., & Schneider, E. (1990). Water mangement and ecological perspectives of the upper rhine’s floodplains. Regulated Rivers: Research & Management, 5(1), 1–15. https://doi.org/10.1002/rrr.3450050102

Dotterweich, M. (2008). The history of soil erosion and fluvial deposits in small catchments of central Europe: Deciphering the long-term interaction between humans and the environment - A review. Geomorphology, 101(1–2), 192–208. https://doi.org/10.1016/j.geomorph.2008.05.023

Dynesius, M., & Nilsson, C. (1994). Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. Science, 266(5186), 753–762. https://doi.org/10.1126/science.266.5186.753

Egger, G., Politti, E., Garófano-Gómez, V., Blamauer, B., Ferreira, M. T., Rivaes, R., … Habersack, H. (2013). Embodying Interactions Between Riparian Vegetation and Fluvial Hydraulic Processes Within a Dynamic Floodplain Model: Concepts and Applications. In Ecohydraulics: An Integrated Approach (pp. 407–427). https://doi.org/10.1002/9781118526576.ch24

Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species’ distributions from occurrence data. Ecography, 29(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Ellenberg, H. (1996). Vegetation Mitteleuropas mit den Alpen (Vol. 1095). https://doi.org/10.1111/j.1654-1103.2012.01443.x

Florsheim, J. L., Mount, J. F., & Chin, A. (2008). Bank Erosion as a Desirable Attribute of Rivers. BioScience, 58(6), 519. https://doi.org/10.1641/B580608

Föll, A., & Egger, G. (2017). Site conditions and potential natural vegetation of the Rhine floodplain near Rastatt. Karlsruhe Institute of Technology (KIT).

Formann, E., Egger, G., Hauer, C., & Habersack, H. (2014). Dynamic disturbance regime approach in river restoration: Concept development and application. Landscape and Ecological Engineering, 10(2), 323–337. https://doi.org/10.1007/s11355-013-0228-5

Franz, E. H., & Bazzaz, F. a. (1977). Simulation of Vegetation Response to Modified Hydrologic Regimes: A Probabilistic Model Based on Niche Differentiation in a Floodplain Forest. Ecology, 58(1), 176–183. https://doi.org/10.2307/1935119

Fuchs, E., Schleuter, M., & Rosenzweig, S. (2012). Integrated Floodplain Response Model (INFORM) as a tool to predict effects of human impacts on habitat availability for floodplain species. River Systems, 20(1–2), 41–53. https://doi.org/10.1127/1868-5749/2012/0031

Gallusser, W. A., & Schenker, A. (1992). Die Auen am Oberrhein, Les zones alluviales du Rhin supérieur. Ausmaß und Perspektiven des Landschaftswandels am südlichen und mittleren Oberrhein seit 1800/Etendue et perspectives de l'évolution des paysages dans le secteur méridional et moyen du Rhin su. Springer.

García-Arias, A., & Francés, F. (2016). The RVDM: modelling impacts, evolution and competition processes to determine riparian vegetation dynamics. Ecohydrology, 9(3), 438–459. https://doi.org/10.1002/eco.1648

Geerling, G. W., Ragas, A. M. J., Leuven, R. S. E. W., van den Berg, J. H., Breedveld, M., Liefhebber, D., & Smits, A. J. M. (2006). Succession and Rejuvenation in Floodplains along the River Allier (France). Hydrobiologia, 565(1), 71–86. https://doi.org/10.1007/s10750-005-1906-6

Gilliam, F. S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. BioScience, 57(10), 845–858. https://doi.org/10.1641/B571007

Glavac, V., Grillenberger, C., Hakes, W., & Ziezold, H. (1992). On the nature of vegetation boundaries, undisturbed flood plain forest communities as an example - a contribution to the continuum/discontinuum controversy. Vegetatio, 101(2), 123–144. https://doi.org/10.1007/BF00033197

Gurnell, A. M. (2016). Hydrogeomorphology- Ecology Interactions in River Systems. River Research and Applications, 22(March 2014), 1085–1095. https://doi.org/10.1002/rra

Gurnell, A. M., & Petts, G. E. (2002). Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology, 47(4), 581–600. https://doi.org/10.1046/j.1365-2427.2002.00923.x

Habersack, H., & Piégay, H. (2007). 27 River restoration in the Alps and their surroundings: past experience and future challenges. Developments in Earth Surface Processes, 11(07), 703–735. https://doi.org/10.1016/S0928-2025(07)11161-5

Hall, G. M. J., & McGlone, M. S. (2006). Potential forest cover of New Zealand as determined by an ecosystem process model. New Zealand Journal of Botany, 44(2), 211–232. https://doi.org/10.1080/0028825X.2006.9513019

Hannon, B., & Ruth, M. (1998). Modeling dynamic biological systems. In Computers & Mathematics with Applications (Vol. 35). https://doi.org/10.1016/S0898-1221(98)90729-5

Härdtle, W. (1995). On the theoretical concept of the potential natural vegetation and proposals for an up-to-date modification. Folia Geobotanica, 30(3), 263–276. https://doi.org/10.1007/BF02803708

Hazelton, E. L. G., Mozdzer, T. J., Burdick, D. M., Kettenring, K. M., & Whigham, D. F. (2014). Phragmites australis management in the United States: 40 years of methods and outcomes. AoB PLANTS, 6, 1–19. https://doi.org/10.1093/aobpla/plu001

Herget, J., & et al., et al. (2005). Engineering impacts on river channels in the River Rhine catchment. Erdkunde, 59(3/4), 294–319. https://doi.org/10.3112/erdkunde.2005.03.07

Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., … Sykes, M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography, 21(1), 50–63. https://doi.org/10.1111/j.1466-8238.2010.00613.x

Hohensinner, S., Habersack, H., Jungwirth, M., & Zauner, G. (2004). Reconstruction of the characteristics of a natural alluvial river-floodplain system and hydromorphological changes following human modifications: The Danube River (1812-1991). River Research and Applications, 20(1), 25–41. https://doi.org/10.1002/rra.719

Hohensinner, S., Jungwirth, M., Muhar, S., & Schmutz, S. (2014). Importance of multi-dimensional morphodynamics for habitat evolution: Danube River 1715-2006. Geomorphology, 215, 3–19. https://doi.org/10.1016/j.geomorph.2013.08.001

Hosner, J. F., & Minckler, L. S. (1963). Bottomland Hardwood Forests of Southern Illinois--Regeneration and Succession. Ecology, 44(1), 29–41.

Hughes, F. M. R. (1988). The ecology of African floodplain forests in semi-arid and arid zones: a review. Journal of Biogeography, 127–140.

Jackson, S. T. (2013). Natural , potential and actual vegetation in North America. 24, 772–776. https://doi.org/10.1111/jvs.12004

Jungwirth, M., Muhar, S., & Schmutz, S. (2002). Re-establishing and assessing ecological integrity in riverine landscapes. Freshwater Biology, 47(4), 867–887. https://doi.org/10.1046/j.1365-2427.2002.00914.x

Justice, C., White, S. M., McCullough, D. A., Graves, D. S., & Blanchard, M. R. (2017). Can stream and riparian restoration offset climate change impacts to salmon populations? Journal of Environmental Management, 188, 212–227. https://doi.org/10.1016/j.jenvman.2016.12.005

Klimas, C., Murray, E., Foti, T., Pagan, J., Williamson, M., & Langston, H. (2009). An ecosystem restoration model for the Mississippi alluvial valley based on geomorphology, soils, and hydrology. Wetlands, 29(2), 430–450. https://doi.org/10.1672/08-99.1

Kowarik, I. (1987). The electronic publication Kritische Anmerkungen zum theoretischen Konzept der potentiellen natürlichen Vegetation mit Anregungen zu einer zeitgemäßen Modifikation has been archived at http://publikationen.ub.uni-frankfurt.de/ (repository of University L. (Kowarik).

Lai, Y. G. (2008). SRH-2D version 2: Theory and User's Manual. Sedimentation and River Hydraulics–Two-Dimensional River Flow Modeling, US Department of Interior, Bureau of Reclamation, November.

Landis, J. R., & Koch, G. G. (1977). The Measurement of Observer Agreement for Categorical Data. Biometrics, 33(1), 159. https://doi.org/10.2307/2529310

Lenders, H. J. R., Leuven, R. S. E. W., Nienhuis, P. H., de Nooij, R. J. W., & Van Rooij, S. A. M. (2001). BIO-SAFE: a method for evaluation of biodiversity values on the basis of political and legal criteria. Landscape and Urban Planning, 55(2), 121–137. https://doi.org/10.1016/S0169-2046(01)00149-9

Leuschner, C. (1997). Das Konzept der potentiellen natürlichen Vegetation (PNV) : Schwachstellen und Entwicklungsperspektiven. Flora, 192(4), 379–391. https://doi.org/10.1016/S0367-2530(17)30809-5

Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. R News, 2(3), 18–22. Retrieved from http://cran.r-project.org/doc/Rnews/

Loidi, J., & Fernández-González, F. (2012). Potential natural vegetation: Reburying or reboring? Journal of Vegetation Science, 23(3), 596–604. https://doi.org/10.1111/j.1654-1103.2012.01387.x

Magilligan, F. J., & Nislow, K. H. (2005). Changes in hydrologic regime by dams. Geomorphology, 71(1–2), 61–78. https://doi.org/10.1016/j.geomorph.2004.08.017

Mahoney, J. M., & Rood, S. B. (1998). Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands, 18(4), 634–645.

Menuz, D. R. (2011). Using Species Distribution Models to Assess Invasion Theory and Provide Management Recommendations for Riparian Areas in the Eastern Columbia and Western Missouri River Basins.

Metzger, F., & Schultz, J. (1984). Understory Response to 50 Years of Management of a Northern Hardwood Forest in Upper Michigan. The American Midland Naturalist, 112(2), 209–223. https://doi.org/10.2307/2425428

Mitchell, F. J. G. (2005). How open were European primeval forests? Hypothesis testing using palaeoecological data. Journal of Ecology, 93(1), 168–177. https://doi.org/10.1111/j.1365-2745.2004.00964.x

Moravec, J. (1998). Reconstructed Natural versus Potential Natural Vegetation in Vegetation Mapping: A Discussion of Concepts. Applied Vegetation Science, 1, 173–176. https://doi.org/10.2307/1478946

Mucina, L. (2010). Floristic-phytosociological approach, potential natural vegetation, and survival of prejudice. Lazaroa, 31(1), 173–182. https://doi.org/10.5209/rev_LAZA.2010.v31.13

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853–858. https://doi.org/10.1038/35002501

Naiman, R. J., & Decamps, H. (1997). The Ecology of Interfaces: Riparian Zones. Annual Review of Ecology and Systematics, 28, 621–658.

Nilsson, C., & Berggren, K. (2000). Alterations of riparian ecosystems caused by river regulation dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our. BioScience, 50(9), 783--792. https://doi.org/10.1641/0006-3568(2000)050[0783:AORECB]2.0.CO;2

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. Science, 308(5720), 405–408. https://doi.org/10.1126/science.1107887

Nixon, E. S., Willett, R. L., & Cox, P. W. (1977). Woody Vegetation of a Virgin Forest in an Eastern Texas River Bottom. Castanea, 42(3), 227–236. Retrieved from http://www.jstor.org/stable/4032817

Ochs, K., Egger, G., Kopecki, I., & Ferreira, T. (2019). Model-based reconstruction of the succession dynamics of a large river floodplain. River Research and Applications, 35(7), 944–954. https://doi.org/10.1002/rra.3502

Ollero, A. (2010). Channel changes and floodplain management in the meandering middle Ebro River, Spain. Geomorphology, 117(3–4), 247–260. https://doi.org/10.1016/j.geomorph.2009.01.015

Oorschot, M. van, Kleinhans, M., Geerling, G., & Middelkoop, H. (2016). Distinct patterns of interaction between vegetation and morphodynamics. Earth Surface Processes and Landforms, 41(6), 791–808. https://doi.org/10.1002/esp.3864

Pearlstine, L., McKellar, H., & Kitchens, W. (1985). Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. Ecological Modelling, 29(1–4), 283–302. https://doi.org/10.1016/0304-3800(85)90057-2

Petts, G. E., & Gurnell, A. M. (2005). Dams and geomorphology: Research progress and future directions. Geomorphology, 71(1–2), 27–47. https://doi.org/10.1016/j.geomorph.2004.02.015

Pieterse, N. M., Olde Venterink, H., Schot, P. P., Wassen, M. J., & Verkroost, A. W. M. (1998). 4. Habitat and Vegetation Response Prediction for Meadows and Fens - Application of SMART-MOVE on a Regional Scale. Demonstration Project for the Development of Integrated Management Plans for Catchment Areas of Small Trans-Border Lowland Rivers: The River Dommel. Report, 4(January), 1–53.

Pontius, R. G. (2000). Quantification error versus location error in comparison of categorical maps. Photogrammetric Engineering and Remote Sensing, Vol. 66, pp. 1011–1016. https://doi.org/Cited By (since 1996) 180 Export Date 10 May 2012

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., … Winterbourn, M. J. (1988). Patch Dynamics in Lotic Systems: The Stream as a Mosaic. Journal of the North American Benthological Society, 7(4), 503–524. https://doi.org/10.2307/1467303

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., … Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography, 40(8), 913–929. https://doi.org/10.1111/ecog.02881

Roberts, J., & Ludwig, J. A. (2016). Riparian Vegetation Along Current-Exposure Gradients in Floodplain Wetlands of the River Murray , Australia Published by : British Ecological Society

Stable URL : http://www.jstor.org/stable/2260787 Accessed : 04-04-2016 04 : 55 UTC Your use of the JSTOR . 79(1), 117–127.

Robertson, P. a., Weaver, G. T., & Cavanaugh, J. a. (1978). Vegetation and Tree Species Patterns near the Northern Terminus of the Southern Floodplain Forest. Ecological Monographs, 48(3), 249–267.

Runhaar, J. (2003). Natuurgericht landevaluatiesysteem (NATLES) versie 2. Alterra-rapport;550. Retrieved from http://library.wur.nl/wasp/bestanden/LUWPUBRD_00321225_A502_001.pdf

Schleupner, C., & Schneider, U. A. (2013). Allocation of European wetland restoration options for systematic conservation planning. Land Use Policy, 30(1), 604–614. https://doi.org/10.1016/j.landusepol.2012.05.008

Schleuter, M. (2014). Computing the degradation of riparian floodplains by means of a water-level difference curve , “ Salix231 ” - a new approach to determine riverbed level variations.

Schleuter, M. (2016). Calculation of flood duration in floodplains by means of a universally applicable formula. 11th ISE 2016, Melbourne, Australia, 711(1), 1–4.

Shi, H., Wen, Z., Paull, D., & Jiao, F. (2016). Distribution of Natural and Planted Forests in the Yanhe River Catchment: Have We Planted Trees on the Right Sites? Forests, 7(12), 258. https://doi.org/10.3390/f7110258

Somodi, I., Molnár, Z., Czúcz, B., Bede-Fazekas, Á., Bölöni, J., Pásztor, L., … Zimmermann, N. E. (2017). Implementation and application of multiple potential natural vegetation models – a case study of Hungary. Journal of Vegetation Science, 28(6), 1260–1269. https://doi.org/10.1111/jvs.12564

Somodi, I., Molnár, Z., & Ewald, J. (2012). Towards a more transparent use of the potential natural vegetation concept - an answer to Chiarucci et al. Journal of Vegetation Science, 23(3), 590–595. https://doi.org/10.1111/j.1654-1103.2011.01378.x

Stanford, J. A., Lorang, M. S., & Hauer, F. R. (2005). The shifting habitat mosaic of river ecosystems. SIL Proceedings, 1922-2010, 29(1), 123–136. https://doi.org/10.1080/03680770.2005.11901979

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. Environmental Conservation, 29(3), 308–330. https://doi.org/10.1017/S037689290200022X

Tuxen, R. (1956). Die heutige potentielle naturliche Vegetation als Gegenstand der Vegetationskartierung. Angewandte Pflanzensoziologie, 13, 5–42.

Uddin, M. N., & Robinson, R. W. (2018). Can nutrient enrichment influence the invasion of Phragmites australis? Science of the Total Environment, 613–614, 1449–1459. https://doi.org/10.1016/j.scitotenv.2017.06.131

Ward, J. V., & Stanford, J. A. (1995). Ecosystems and Its Disruption By Flow Regulation. Regulated Rivers: Research & Management, II(July 1994), 105–119. https://doi.org/10.1002/rrr.3450110109

Wasserstrassen- und Schifffahrtsverwaltung des Bundes (WSV). (2016). Digitales Geländemodell des Wasserlaufs (DGM-W). Retrieved from https://www.govdata.de/daten/-/details/1c669080-c804-11e4-8731-1681e6b88ec1bkg

Wenger, S. J., & Olden, J. D. (2012). Assessing transferability of ecological models : an underappreciated aspect of statistical validation. 260–267. https://doi.org/10.1111/j.2041-210X.2011.00170.x

Westhoff, V., & Van Der Maarel, E. (1978). The braun-blanquet approach. In Classification of plant communities (pp. 287–399). Springer.

Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S., & Stanford, J. A. (2007). Climate, hydrologic disturbance, and succession: Drivers of floodplain pattern. Ecology, 88(4), 940–953. https://doi.org/10.1890/05-1149

Willis, K. J., & Birks, H. J. B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. Science, 314(5803), 1261–1265. https://doi.org/10.1126/science.1122667

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Zerbe, S. (1998). Potential natural vegetation: validity and applicability in landscape planning and nature conservation. Applied Vegetation Science, 1(2), 165–172. https://doi.org/10.2307/1478945

6 CONCLUSION

Under the premise of the goals of the FLUVIO doctoral program and the awareness that for restoration and management of the riverine ecosystem it is fundamental to understand and predict the spatial patterns of its vegetation the presented Ph.D. research had the overall objective to explore different modeling approaches that could help river managers to make predictions about the distribution of riverine vegetation in regulated river systems. The underlying research question was how river regulation affects the patterns of aquatic and riparian vegetation and whether the assumption of equilibrium between vegetation and environmental factors inherent of static models can be justified due to the reduction of fluvial dynamics.

In Chapter 2 of this thesis a systematic, quantitative literature review in English speaking journals on models to predict the distribution of riverine vegetation on reach scale was performed with the aim to give a comprehensive overview of the model landscape and identify research gaps to guide the further development of the thesis. One of the results was that the number of models to predict the distribution of riverine vegetation is increasing across the globe but that current research is disproportionately focused on riparian vegetation and towards rivers in developed nations as well as temperate and mediterranean habitats of the northern hemisphere. We also observed that despite the recognition that the riverine ecosystem is disturbance driven over one-third of all models were based on the assumption of equilibrium between environmental factors and vegetation distribution which led us to the overall research question of whether this might be a justified simplification because of river regulation. Additionally, we detected a lack of models that consider the simulation of succession and competition which have to be regarded dominant processes in the largest parts of most floodplains and a lack of models that consider the feedbacks between hydro-morphology and riverine vegetation. Also, less than 10% of all models were validated against spatial independent data.

Chapter 3 is a reaction to the diagnosed lack of models for aquatic vegetation. It contributed to the overall research question through the development and testing of a habitat suitability model for aquatic vegetation based on hydrological variables to study the effect of artificially stabilized (static) low flows during the vegetation period on the invasion and proliferation of aquatic vegetation. Although the high sensitivity of aquatic vegetation to the instream hydraulic condition is known models for aquatic vegetation based on hydrological variables and management approaches based on flow regulation are relatively unexplored. Through field measurements of species presence/absence and the parameters flow velocity, water depth and substrate it was possible to build a habitat suitability model for the invasive *Myriophyllum aquaticum* as well as the most frequent native species *Potamogetum crispus* and *Sparganium ercetum*, that showed high accuracy against spatial independent presence/absence data. The good accuracy of the habitat suitability model indicates that the distribution of macrophytes during the vegetation period is in equilibrium with the artificially stabilized hydraulic condition. Further, through the coupling of the habitat suitability model with a two-dimensional hydraulic model, it was possible to determine minimum annual flows that reduce the habitat of the invader *Myriophyllum aquaticum* while simultaneously promoting that of native species. Which led to the conclusion that maintaining minimum discharges above a certain threshold in order to prevent channel encroachment may be an ecologically and financially advantageous addition to the range of commonly practiced control measures.

Chapter 4 contributed to the thesis objective by investigating the effects of the extreme reduction of hydro-geomorphological disturbances that most European large rivers suffered during the last centuries on the succession trajectory of the floodplain vegetation through the use of a dynamic succession model. Based on historic maps and discharge time series we presented a novel methodology for the parametrization of the dynamic model CASiMiR Vegetation and were able to reconstruct the succession dynamics of a large European river in a high spatial and temporal resolution. This is of special interest because long-term observations of the development of the flood plain vegetation of large rivers are extremely rare and difficult to interpret because of the high degree of direct modification of the actual vegetation through agriculture and forestry. Through the simulation we found out that due to a lack of fluvial disturbances strong enough to reset succession vegetation communities demonstrated a steady progression toward mature phases without regression to younger stages and that the habitat progression slows down over time as more habitat remains changeless towards the end of the simulation period. Physiological stress caused by long inundations periods was the most relevant controlling factor of succession. We argued that the resulting vegetation distribution (2016) can be considered an estimation of the potential natural vegetation (PNV) under altered site conditions and that the good agreement of the model results with an expert-based PNV map showed that our approach is an alternative to create benchmark maps for floodplain conservation and restoration projects which has the big advantage over the traditional approach that it allows analyzing different points in time as well as to be comprehensive and reproducible.

The thesis culminated in chapter 5 where we, based on the observations in chapters 2 and 4, directly addressed the question of whether the consideration of succession dynamics and disturbance stochasticity are still relevant to model vegetation patterns of regulated large river floodplains. To answer it we compared the results of the simulation of the vegetation succession from chapter 4 to different statistic and expert-based modeling approaches for the distribution of floodplain vegetation for the same area and discussed them in regard to the concept of Potential Natural Vegetation (PNV). The validation of the different PNV estimation methods against a set of independent reference plots and the direct comparison of their results revealed very similar performances. The most important predictor of PNV, identified by all approaches, is flood duration. But the resulting pattern of softwood, transition and hardwood forest is explained equally well by a static average as a reconstruction of the temporal dynamics of the flood regime. We therefore conclude that due to a lack of disturbances, the vegetation of regulated large rivers has indeed reached a near-equilibrium state with the altered hydrologic regime and that a static perception of its PNV seems reasonable.

Consequently, from a manager´s perspective, in artificially stabilized environments, such as the Sorraia river in Portugal (chapter 3) or the Rhine River in Germany (chapter 4 and 5) static models based on an equilibrium assumption seem to be an adequate option for the modeling of the distribution of riverine vegetation since they show high accuracy, need relatively few resources (data, time, expert knowledge) and are still comprehensive and reproducible.

6.1 Ways forward

The modeling of the distribution of riverine vegetation is a very complex topic due to the various interactions between vegetation and fluvial process and in this thesis it was only possible to focus on a small subsection. However, during the course of research other issues regarding the modeling of the distribution of riverine vegetation have been identified that deserve a more detailed examination. Therefore we want to present the following recommendations for further research:

- Extension of research to the southern hemisphere and to river systems of other biomes than the temperate and Mediterranean climate. The tropical and subtropical regions where the world’s most biodiverse river basins (the Amazon, Congo, and Mekong) can be found and that are experiencing an boom in the construction of hydropower dams would be an interesting area for model development and application.

- Model development to predict the distribution of aquatic vegetation considering fluvial dynamics as spatial decision support for environmental management on reach scale.

- Further research is needed to understand the effect of stochastic variability of river discharge and, in regard to riparian vegetation of groundwater flow (spatial-temporal dynamics of soil moisture and of water table) on vegetation patterns.

- More models need to be developed that account for competition and facilitation processes since they directly control the dominance of specific species by resource competition and the creation of favorable settlement conditions for other species by facilitation. These process become especially important in the context of species invasions which rivers are particularly prone to.

- Development of models that incorporate the direct interactions of vegetation with geo-morphodynamic processes such as interactions between vegetation and the flow field and its implications on sediment transport as well as the interaction between river bank accretion and vegetation dynamics. Of particular interest is facilitation by ecosystem engineers (e.g. *Salicaceae specie, Sparganium erectum*) that modify the flow field and trap sediments around (point) bars because it is an important process to take into account for the prediction of vegetation distribution and river planform development in natural river systems.

- Testing of model reliability through validation against independent data from different geographic regions or spatially distinct subsets of the region or different time periods.

APPENDIX A – CASIMIR VEGETATION PARAMETER

Historic land-use				Starting condition (1872)		
1816	1838	1852	1872	Succession phase	Age	Succession line
-	Gravel	Forest	Forest	ESWP	33	Sand aggradation line
-	Water	Forest	Forest	ESWP	33	Silt aggradation line
-	-	Gravel	Forest	ESWP	19	Sand aggradation line
-	-	Water	Forest	ESWP	19	Silt aggradation line
Forest	Forest	Forest	Forest	EFP	100	Sand aggradation line
-	-	-	Grass-land, agriculture areas	HP	1	Secondary succession
-	-	-	Gravel-, sand-bank	IP	1	Sand aggradation line
-	-	-	Other forests	ESWP	33	Sand aggradation line

Table A 1: Deduction of the starting condition derived from the analysis of the chronological sequence of forest, gravel and water surfaces on historical maps (Abbreviations: IP, Initial Phase; HP, Herb Phase; ESWP, Early Successional Woodland Phase; EFP, Established Forest Phase).

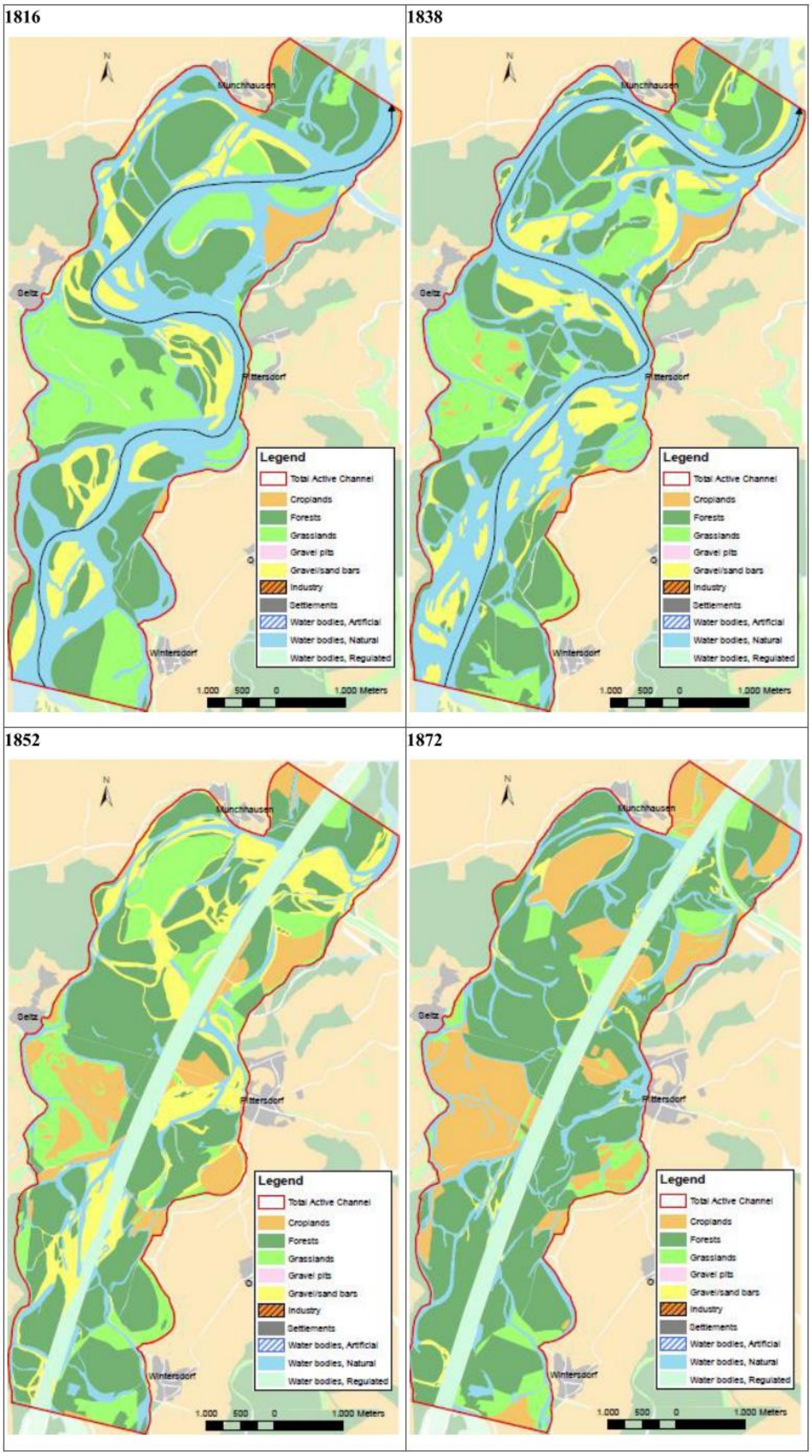

Figure A 1: Historic maps used to reconstruct the model starting condition

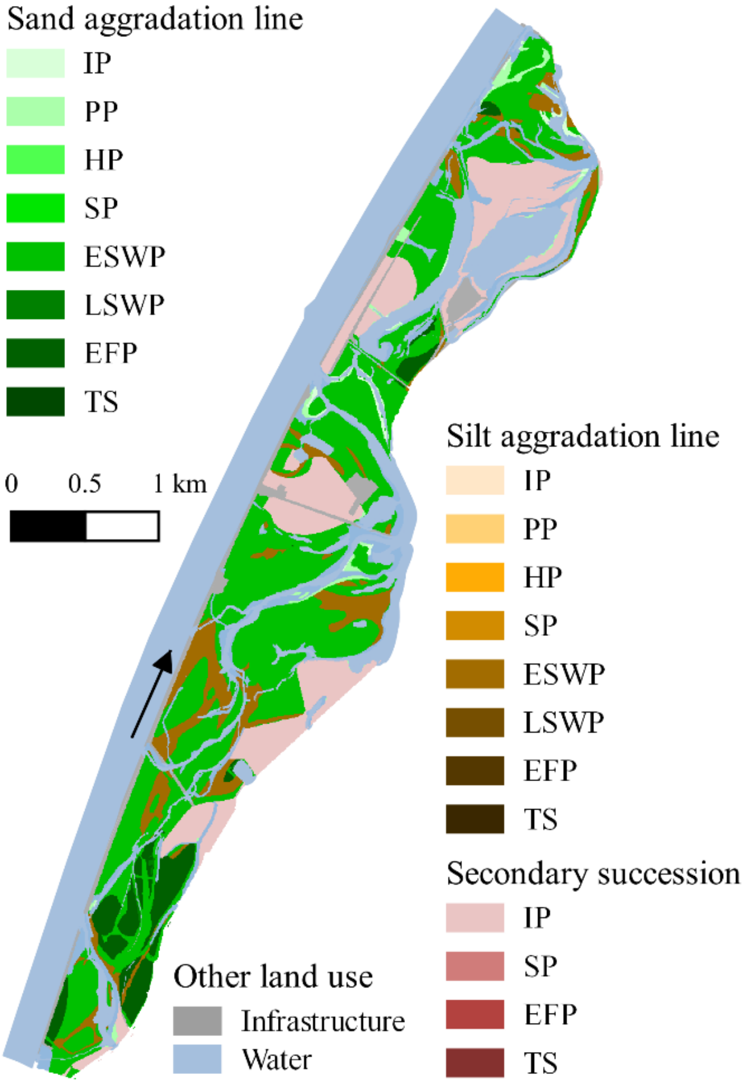

Figure A 2: Starting condition (1872) used as model input. It was derived from the analysis of the chronological sequence of forest, gravel and water surfaces on historical maps. Abbreviations: IP, Initial Phase; PP, Pioneer Phase; HP, Herb Phase; SP, Shrub Phase; ESWP, Early Successional Woodland Phase; LSWP, Late Successional Woodland Phase; EFP, Established Forest Phase; TS, Terminal Stage

Succession lines	Phase	Age / life span without disturbance (years)
Sand aggradation line	IP	0-1
	PP	2-3
	HP	4-9
	SP	10-15
	ESWP	16-59
	LSWP	60-99
	EFP	100-139
	TS	140-1000
Silt aggradation line	SW	20
	IP	0-1
	PP	2-3
	HP	4-15
	SP	16-25
	ESWP	26-69
	LSWP	70-109
	EFP	110-159
	TS	160-1000
Secondary succession	HP	0-5
	SP	6-29
	EFP	30-79
	TS	80-1000

Table A 2: Succession lines, phases and age spans of the vegetation model. Abbreviations: IP, Initial Phase; PP, Pioneer Phase; HP, Herb Phase; SP, Shrub Phase; ESWP, Early Successional Woodland Phase; LSWP, Late Successional Woodland Phase; EFP, Established Forest Phase; TS, Terminal Stage

Succession lines	Bank zone		Floodplain zone	
	Min. water level (m)	Max. water level (m)	Min. water level (m)	Max. water level (m)
Sand aggradation line	1	5	1	5
Silt aggradation line	7	1000	7	1000
Secondary succession	1	5	1	5

Table A 3: Water levels for the bank and floodplain zone that allow recruitment. The maximum water levels of the silt aggradation lines are chosen so high that potential outliers will be included

Succession phase	Disturbance class – shear stress				
	Very low (0.1 - 2 N/m²)	low (2 - 5 N/m²)	medium (5 - 50 N/m²)	strong (50 - 200 N/m²)	Very strong (> 200 N/m²)
IP	no effect	remains in IP	remains in IP	remains in IP	remains in IP
PP	no effect	no effect	remains in PP	set back to IP	set back to IP
HP	no effect	no effect	remains in HP	set back to PP	set back to IP
SP	no effect	no effect	no effect	remains in SP	set back to IP
ESWP	no effect	no effect	no effect	remains in ESWP	set back to IP
LSWP	no effect	no effect	no effect	remains in LSWP	set back to IP
EFP	no effect	no effect	no effect	remains in EFP	set back to IP
TS	no effect	no effect	no effect	remains in TS	set back to IP

Table A 4 : Expert rules of the vegetation model controlling succession for the disturbance indicator shear stress

Succession phase	Disturbance class – flood duration				
	Very low (0-5 days)	low (5-20 days)	medium (20-70 days)	strong (70-120 days)	Very strong (110-183 days)
IP	no effect	no effect	remains in IP	remains in IP	remains in IP
PP	no effect	no effect	remains in PP	set back to IP	set back to IP
HP	no effect	no effect	no effect	remains in HP	set back to PP
SP	no effect	no effect	no effect	remains in SP	set back to PP
ESWP	no effect	no effect	no effect	no effect	remains in ESWP
LSWP	no effect	no effect	remains in LSWP	remains in LSWP	set back to ESWP
EFP	no effect	remains in EFP	remains in EFP	set back to LSWP	set back to LSWP
TS	no effect	remains in TS	remains in TS	set back to EFP	set back to LSWP

Table A 5: Expert rules of the vegetation model controlling succession for the disturbance indicator flood duration

APPENDIX B - MAIN PNV-TYPES AND THEIR INDICATOR SPECIES

PNV-Type I	PNV-Type II	Forest layer	Indicator species
Reeds	Pioneer vegetation	TL	-
		SL	-
		HL	Mentha aquatica
			Symphytum officinale
	Reeds and natural grasslands	TL	-
		SL	-
		HL	Phragmites australis
			Agrostis gigantea
			Calystegia sepium
			Galium aparine
Softwood Forests	Willow shrubs	TL	-
		SL	Salix alba
			Salix purpurea
			Salix viminalis
		HL	Mentha aquatica
			Myosotis palustris
	Salicetum albae	TL	Salix alba
		SL	Salix alba
		HL	Myosotis palustris

			Rhorippa amphibia
			Senetio paludosus
			Mentha aquatica
			Phalaris arundinacea
			Myosotis palustris
			Rubus caesius
			Galium palustre
			Phragmites australis
			Rorippa amphibia
			Symphytum officinale
Transition Forest	Salicitum albae - Querco-Ulmetum	TL	Salix alba
		SL	Cornus sanguinea
			Viburnum opulus
			Crataegus monogyna
		HL	Rubus caesius
			Phalaris arundinacea
Hardwood forest	Querco-Ulmetum	TL	Fraxinus excelsior
			Acer platanoides
			Quercus robur
			Acer campestre
			Alnus incana
		SL	Cornus sanguinea

			Crataegus monogyna
			Viburnum opulus
			Ligustrum vulgare
			Corylus avellana
		HL	Rubus caesius
			Galium aparine
			Hedera helix
			Impatiens glandulifera
			Paris quadrifolia
			Viola reichenbachiana
	Stellario - Carpinetum	TL	Carpinus betulus
			Acer Campestre
			Quercus robur
		SL	Corylus avellana
		HL	Allium ursinium
			Stellaria holesta

Table B 1: Main PNV-types, forest layer (TL – tree layer, SL – shrub layer, HL – herb layer) and their indicator species (Dister, 1980)

APPENDIX C - CALCULATION OF FLOOD DURATION

Map representations of flood duration were needed as input for the DM and static models. For the DM five representative years (dry, medium wet, wet, very wet and extreme wet) from the period 1921-2016 were selected based on their maximum, mean and minimum discharge and the representativeness of the flow duration curve (Table C 1). For the SM the average flood duration of the vegetation period (1921-2016) was considered. To reduce the calculational efforts for the hydrodynamic modeling, 14 discharges were selected to best represent the average flow duration curve of the vegetation period (Table C 2). Using the two-dimensional hydrodynamic model, the water surface elevations (WSE) for these 14 discharges were calculated for the whole study area. In a first step the results from the irregular hydrodynamic model mesh were transferred into raster (regular grids). For the calculation of the flood duration raster of each representative year we attributed to the WSE of the 14 modeled discharges the number of days that they were exceeded during the growing period through analyzing the respective hydrographs (Table C 2).

Year	Category	Max. Discharge	Mean Discharge	Min. discharge	Discharge >= 2000 m³/s (days)
1999	extremely wet	4330	1917	818	-
1965	very wet	3530	2048	1260	> 80
1978	wet	4140	1698	862	45 - 79
1985	medium	2720	1419	686	8 - 44
1943	dry	2140	1087	622	0 - 7

Table C 1: Representative years for the calculation of the flood duration raster, their category and criteria for selection

Discharge (m^3/s)	Character	Days exceeded in year category				
		dry	medium	wet	very wet	extremely wet
609	Other	183	183	183	183	183
1257	MQ	39	112	135	183	147
1600	Other	14	63	96	149	111
2000	Other	2	8	46	99	66
2200	Other	0	5	20	67	53
2450	Other	0	2	12	40	39
2724	HQ1	0	0	8	13	35
2850	HQ2	0	0	7	7	29
3000	Other	0	0	6	4	21
3150	Other	0	0	5	3	13
3594	HQ5	0	0	3	0	7
4100	HQ10	0	0	1	0	3
4900	HQ50	0	0	0	0	0
5300	HQ100	0	0	0	0	0

Table C 2: Characteristic discharges and the numbers of days each is exceeded in the vegetation period of each representative year category

The final raster was then composed through superimposing the WSE of each modelled discharge and their number of days exceeded. The flood duration of the grid cell located between the water edge lines of two neighboring WSE was calculated according to the relative vertical position of the grid cell between the two calculated water surface elevation, as shown in Figure C 1: and the following equation:

$$FD_n = FD_{Q1} - \Delta FD \frac{(z_n - WSE_{Q1})}{(WSE_{Q2} - WSE_{Q1})}$$

with

FD_n = *flood duration of grid cell n located between the water edge of flow rate Q1 and flow rate Q2, [days]*

FD_{Q1} = *flooding duration for flow rate Q1 [days]*

ΔFD = *difference between flooding duration for flow rate Q1 and Q2 [days]*

z_n = *terrain elevation of grid cell n, [meter above sea level]*

WSE_{Q1} = *Water surface elevation for flow rate Q1 (extrapolated,) [meter above sea level]*

WSE_{Q2} = *Water surface elevation for flow rate Q2, [meter above sea level]*

Eq. C 1: Calculation of the flood duration of a grid cell located between the water edges of two modeled discharges

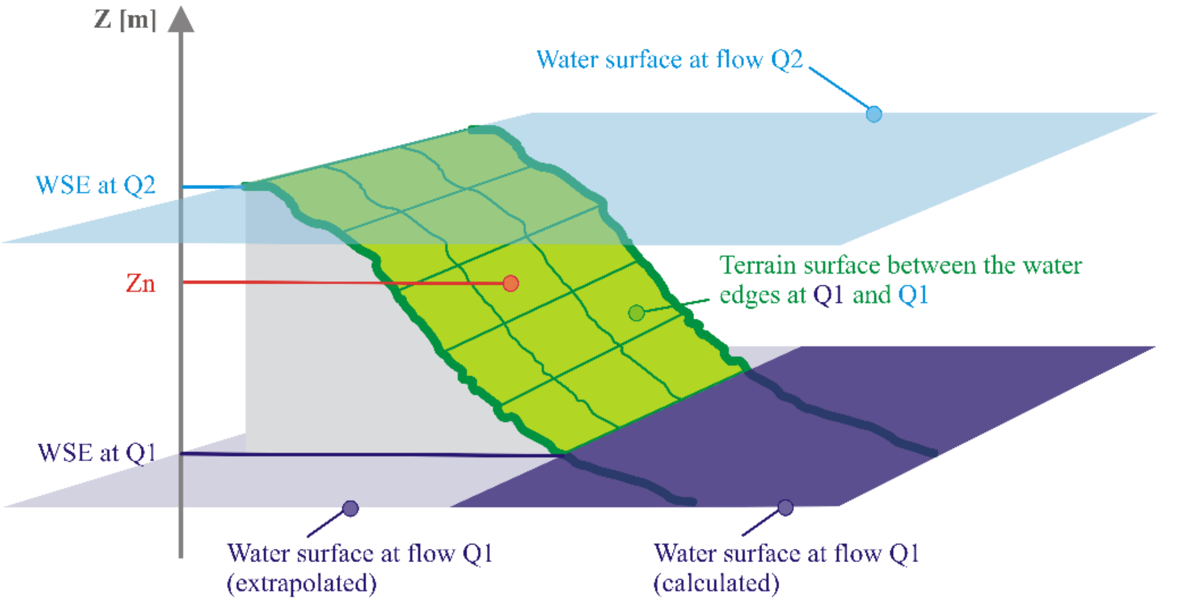

Figure C 1: Illustration for the calculation of the flood duration of a grid cell located between the water edges of two modeled discharges (Eq. C 1)

APPENDIX D – DATABASE OF MODELS OF SPATIAL DISTRIBUTION OF RIVERINE VEGETATION ON REACH SCALE (SUMMARIZED)

Citation	Research goal	Country	Biome	Catch-ment size	Alti-tude	Regulation measures	Model app-roach	Response level	Vegetation Processes	Variables affecting vegetation	Validation
Tinoco, A. I., Furman, B. T., Darnell, K. M., and Peterson, B. J. (2017). Submerged aquatic vegetation, topography and flow characteristics in the upper, tidal Hudson River: Progress toward a predictive habitat model. Aquat. Bot. 142, 53–60. doi:10.1016/j.aquabot.2017.06.006.	Theoretical ecology	USA	Temperate Broadleaf & Mixed Forests	Very Large	low	Flow regulation	Correlative (static)	Single species	none	Water attributes, flow regime	Hold out (geo.)
Zefferman, E. P., and Harris, D. J. (2016). Predicting drivers of nuisance macrophyte cover in a regulated California stream using boosted regression tree models. J. Aquat. Plant Manag. 54, 78–86.	Conservat-ion planning	USA	Mediterranean Forests, Woodlands & Scrub	Large	mid	Flow regulation	Correlative (static)	Species group	none	Climate, soil attributes, flow regime	Hold out (geo.)
Spencer, D. F., and Carruthers, R. I. (2013). Predicting Eurasian watermilfoil's (Myriophyllum spicatum) distribution and its likely response to biological control in a spring-fed river. J. Aquat. Plant Manag. 51, 7–14.	Conservat-ion planning	USA	Temperate Conifer Forests	Large	high	Flow regulation	Correlative (static)	Single species	none	Water attributes	none
Sousa, W. T. Z., Thomaz, S. M., Murphy, K. J., Silveira, M. J., and Mormul, R. P. (2009). Environmental predictors of the occurrence of exotic Hydrilla	Theoretical ecology	Brazil	Tropical & Subtropical Moist Broadleaf	Very large	mid	Flow regulation	Correlative (static)	Single species	None	Water attributes, soil attributes	Hold out (geo.)

verticillata (L.f.) Royle and native Egeria najas Planch. in a sub-tropical river floodplain: the Upper River Paraná, Brazil. Hydrobiologia 632, 65–78. doi:10.1007/s10750-009-9828-3.			Forests								

Table D 1: Database of scientific publications regarding models for the distribution of aquatic vegetation on reach scale

Citation	Research goal	Country	Biome	Catch-ment size	Alti-tude	Regulation measures	Model app-roach	Response level	Vegetation Processes	Variables affecting vegetation	Validation
García-Arias, A., and Francés, F. (2016). The RVDM: modelling impacts, evolution and competition processes to determine riparian vegetation dynamics. Ecohydrology 9, 438–459. doi:10.1002/eco.1648.	Model develop-ment	Spain	Mediterranean Forests, Woodlands & Scrub	Medium	High	Free flowing	Process-equation-based	Species group	Recruitment, succession, growth, competition, mortality	Soil, flow regime, topographic, climate	hold out (temp.)
Franz, E. H., and Bazzaz, F. a (1977). Simulation of Vegetation Response to Modified Hydrologic Regimes: A Probabilistic Model Based on Niche Differentiation in a Floodplain Forest. Ecology 58, 176–183. doi:10.2307/1935119.	Impact assessment	USA	Temperate Grasslands, Savannas & Shrublands	Large	Low	Flow regulation	Correlative (static)	Single species	none	Topographic	none

Pearlstine, L., McKellar, H., and Kitchens, W. (1985). Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. Ecol. Modell. 29, 283–302. doi:10.1016/0304-3800(85)90057-2.	Impact assessment	USA	Temperate Grasslands, Savannas & Shrublands	Large	Mid.	Flow regulation, channelization	Process-equation-based	Species group	Recruitment, growth, mortality	Soil, topographic, flow regime	independent
Auble, G. T., Friedman, J. M., and Scott, M. L. (1994). Relating Riparian Vegetation to Present and Future Streamflows. Ecol. Appl. 4, 544–554. doi:10.2307/1941956.	Impact assessment	USA	Deserts & Xeric Shrublands	Very large	High	Flow regulation	Correlative (static)	Species group	None	Flow regime	none
Toner, M., and Keddy, P. (1997). River hydrology and riparian wetlands: A predictive model for ecological assembly. Ecol. Appl. 7, 236–246. doi:10.1890/1051-0761(1997)007[0236:RHARWA]2.0.CO;2.	Model develop-ment	Canada	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation	Correlative (static)	Species group	None	Flow regime	resubstitution
Loheide, S. P., and Gorelick, S. M. (2007). Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. Water Resour. Res. 43, 1–16. doi:10.1029/2006WR005233.	Theoretical ecology	USA	Temperate Conifer Forests	Small	High	Flow regulation	Process-equation-based	Species group	Mortality	Hydrologic	none
Hanson, J. S., Malanson, G. P., and Armstrong, M. P. (1990). Landscape fragmentation and dispersal in a model of riparian forest dynamics. Ecol. Modell. 49, 277–296. doi:10.1016/0304-3800(90)90031-B.	Model develop-ment	None	None	None	None	None	Process-equation-based	Single species	Dispersal, recruitment, growth, mortality	Soil, topographic, flow regime	none
Harper, E. B., Stella, J. C., and Fremier, A. K. (2011). Global sensitivity analysis for complex ecological models: a case study of riparian cottonwood population dynamics. Ecol. Appl. 21, 1225–40.	Model develop-ment	USA	Mediterranean Forests, Woodlands & Scrub	Very large	Low	Flow regulation	Process-rule-based	Single species	Recruitment, growth	Topography, flow regime	hold out (geo.)

doi:10.1890/10-0506.1.											
Schaepman, M. E., Wamelink, G. W. W., van Dobben, H. F., Gloor, M., Schaepman-Strub, G., Kooistra, L., et al. (2007). River Floodplain Vegetation Scenario Development Using Imaging Spectroscopy Derived Products as Input Variables in a Dynamic Vegetation Model. Photogramm. Eng. Remote Sens. 73, 1179–1188. doi:10.14358/PERS.73.10.1179.	Model develop-ment	Nether-lands	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation and channelization	Process-equation-based	Species group	Growth, succession, competition	Management, soil	none
Baptist, M. J., Penning, W. E., Duel, H., Smits, A. J. M., Geerling, G. W., Van der Lee, G. E. M., et al. (2004). Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Res. Appl. 20, 285–297. doi:10.1002/rra.778.	Impact assessment	Nether-lands	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation and channelization	Process-rule-based	Species group	Succession	Flow regime, management	none
Kooistra, L., Wamelink, W., Schaepman-Strub, G., Schaepman, M., van Dobben, H., Aduaka, U., et al. (2008). Assessing and predicting biodiversity in a floodplain ecosystem: Assimilation of net primary production derived from imaging spectrometer data into a dynamic vegetation model. Remote Sens. Environ. 112, 2118–2130. doi:10.1016/j.rse.2007.10.010.	Conservat-ion planning	Nether-lands	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation and channelization	Process-equation-based	Species group	Growth, competition, mortality, succession	Management, soil, groundwater regime	resubstitution

Aggenbach, C. J. S., and Pelsma, T. A. H. M. (2003). Hydro-ecological assessment of vegetation of Dutch river habitats. River Syst. 15, 199–210. doi:10.1127/lr/15/2003/199.	Conservation planning	Netherlands	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation, channelization	Expert-based (static)	Species group	None	Soil, flow regime, groundwater regime, management	none
Asaeda, T., Rashid, M. H., & Abu Bakar, R. (2015). Dynamic Modelling of Soil Nitrogen Budget and Vegetation Colonization in Sediment Bars of a Regulated River. River Research and Applications, 31(4), 470–484. https://doi.org/10.1002/rra.2802	Theoretical ecology	Japan	Temperate Broadleaf & Mixed Forests	Large; 2400 km2	Low	Flow regulation	Process-rule-based	Species group	Recruitment, growth, mortality,	Flow regime, topographic, soil	resubstitution
Sanjaya, K., & Asaeda, T. (2017). Application and assessment of a dynamic riparian vegetation model to predict the spatial distribution of vegetation in two Japanese river systems. Journal of Hydro-Environment Research, 16, 1–12. https://doi.org/10.1016/j.jher.2017.05.001	Method evaluation	Japan	Temperate Broadleaf & Mixed Forests	large	low	flow regulation					independent
		Japan	Temperate Broadleaf & Mixed Forests	large; 2400 km4	low	flow regulation					independent
Benjankar, R., Egger, G., Jorde, K., Goodwin, P., and Glenn, N. F. (2011). Dynamic floodplain vegetation model development for the Kootenai River, USA. J. Environ. Manage. 92, 3058–3070. doi:10.1016/j.jenvman.2011.07.017.	Model development	USA	Temperate Conifer Forests	Large	Mid	Flow regulation	Process-rule-based	Species group	Recruitment, growth, succession, mortality	Flow regime, topographic	resubstitution
García-Arias, A., Francés, F., Ferreira, M. T., Egger, G., Martínez-Capel, F., Garófano-Gómez, V., … Rodríguez-González, P. M. (2013). Implementing a dynamic	Method evaluation	Austria,	Temperate Broadleaf & Mixed Forests	large	mid	flow regulation					hold out (temp.)

riparian vegetation model in three European river systems. Ecohydrology, 6(4), 635–651. https://doi.org/10.1002/eco.1331		Spain	Mediterranean Forests, Woodlands & Scrub	medium	high	free flowing					hold out (temp.)
		Portugal	Mediterranean Forests, Woodlands & Scrub	medium	low	free flowing					hold out (temp.)
Rivaes, R., Rodríguez-González, P. M., Ferreira, M. T., Pinheiro, A. N., Politti, E., Egger, G., … Francés, F. (2014). Modeling the evolution of riparian woodlands facing climate change in three european rivers with contrasting flow regimes. PLoS ONE, 9(10). https://doi.org/10.1371/journal.pone.0110200	Climate change	same reaches as above	same reaches as above	same reaches as above	same reaches as above	same reaches as above					
Politti, E., Egger, G., Angermann, K., Rivaes, R., Blamauer, B., Klösch, M., … Habersack, H. (2014). Evaluating climate change impacts on Alpine floodplain vegetation. Hydrobiologia, 737(1), 225–243. https://doi.org/10.1007/s10750-013-1801-5	Climate change	same reach as above	same reach as above	same reach as above	same reach as above	same reach as above					
Rivaes, R., Boavida, I., Santos, J. M., Pinheiro, a. N., & Ferreira, M. T. (2015). The inbuilt long-term unfeasibility of environmental flows when disregarding riparian vegetation requirements. Hydrology and Earth System Sciences Discussions, 12(10), 10701–10737.	Impact assessment	Portugal	Mediterranean Forests, Woodlands & Scrub	Medium	Mid	Flow regulation					hold out (temp.)

https://doi.org/10.5194/hessd-12-10701-2015											
Rivaes, R., Rodríguez-González, P. M., Albuquerque, A., Pinheiro, A. N., Egger, G., & Ferreira, M. T. (2015). Reducing river regulation effects on riparian vegetation using flushing flow regimes. Ecological Engineering, 81, 428–438. https://doi.org/10.1016/j.ecoleng.2015.04.059	Impact assessment	Portugal	Mediterranean Forests, Woodlands & Scrub	Large	Mid	Flow regulation					hold out (temp.)
		Portugal	Mediterranean Forests, Woodlands & Scrub	Large	Mid	Flow regulation					hold out (temp.)
Benjankar, R., Jorde, K., Yager, E. M., Egger, G., Goodwin, P., & Glenn, N. F. (2012). The impact of river modification and dam operation on floodplain vegetation succession trends in the Kootenai River, USA. Ecological Engineering, 46, 88–97. https://doi.org/10.1016/j.ecoleng.2012.05.002	Impact assessment	same as above	same as above	same as above	same as above	same as above					
Egger, G., Politti, E., Woo, H., Cho, K.-H., Park, M., Cho, H., … Lee, H. (2012). Dynamic vegetation model as a tool for ecological impact assessments of dam operation. Journal of Hydro-Environment Research, 6(2), 151–161. https://doi.org/10.1016/j.jher.2012.01.007	Impact assessment	Korea	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation					resubstitution
Hettrich, A., and Rosenzweig, S. (2003). Multivariate statistics as a tool for model-based prediction of floodplain vegetation and fauna. Ecol. Modell. 169,	Model development	Germany	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation, channelizat	Correlative (static)	Single species	None	Flow regime, groundwater regime, soil	resubstitution

73–87. doi:10.1016/S0304-3800(03)00263-1.						ion					
Oorschot, M. van, Kleinhans, M., Geerling, G., and Middelkoop, H. (2016). Distinct patterns of interaction between vegetation and morphodynamics. Earth Surf. Process. Landforms 41, 791–808. doi:10.1002/esp.3864.	Theoretical ecology	France	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation	Process-equation-based	Single species	Recruitment, growth, mortality, sedimentation/erosion, uprooting		resubstitution
van Oorschot, M., Kleinhans, M. G., Geerling, G. W., Egger, G., Leuven, R. S. E. W., & Middelkoop, H. (2017). Modeling invasive alien plant species in river systems: Interaction with native ecosystem engineers and effects on hydro-morphodynamic processes. Water Resources Research, 53(8), 6945–6969. https://doi.org/10.1002/2017WR020854	Theoretical ecology	same as above	same as above	same as above	same as above	same as above					none
Chiarello, E., Amoros, C., Pautou, G., and Jolion, J.-M. (1998). Succession modeling of river floodplain landscapes. Environ. Model. Softw. 13, 75–85. doi:10.1016/S1364-8152(97)00034-0.	Model development	France	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation, channelization	Correlative	Species group	None	Topographic	None
Chen, Q., and Ye, F. (2008). "Unstructured Cellular Automata and the Application to Model River Riparian Vegetation Dynamics," in Cellular Automata (Berlin, Heidelberg: Springer Berlin Heidelberg), 337–344. doi:10.1007/978-3-540-79992-4_43.	Model development	China	Tropical & Subtropical Moist Broadleaf Forests	Very large	Low	Flow regulation, channelization	Process-equation-based	Single species	recruitment, growth, competition, mortality	Flow regime	None

Ye, F., Chen, Q., and Li, R. (2010). Modelling the riparian vegetation evolution due to flow regulation of Lijiang River by unstructured cellular automata. Ecol. Inform. 5, 108–114. doi:10.1016/j.ecoinf.2009.08.002.	Impact assessment	same as above	same as above	same as above	same as above	same as above					None
Liu, D., Tian, F., Hu, H., Lin, M., and Cong, Z. (2012). Ecohydrological evolution model on riparian vegetation in hyperarid regions and its validation in the lower reach of Tarim River. Hydrol. Process. 26, 2049–2060. doi:10.1002/hyp.8313.	Model development	China	Deserts & Xeric Shrublands	Large	High	Flow regulation	Process-equation-based	Species group	Colonization, mortality	Groundwater regime, soil	None
van Ek, R., Witte, J.-P. M., Runhaar, H., & Klijn, F. (2000). Ecological effects of water management in the Netherlands: the model DEMNAT. Ecological Engineering, 16(1), 127–141. https://doi.org/10.1016/S0925-8574(00)00097-5	Model development	Netherlands	Temperate Broadleaf & Mixed Forests	Very large	Low	Flow regulation, channelization	Expert-based (static)	Species group	None	Groundwater regime, soil	resubstitution
Hoffman, J. D., Narumalani, S., Mishra, D. R., Merani, P., & Wilson, R. G. (2008). Predicting Potential Occurrence and Spread of Invasive Plant Species along the North Platte River, Nebraska. Invasive Plant Science and Management, 1(4), 359–367. https://doi.org/10.1614/IPSM-07-048.1	Conservation planning	USA	Temperate Grasslands, Savannas & Shrublands	Very large	High	Flow regulation	Correlative	Single species	None	Topographic, soil, management	hold out (geo.)
Hooke, J. M., Brookes, C. J., Duane, W., & Mant, J. M. (2005). A simulation model of morphological, vegetation and sediment changes in ephemeral streams. Earth Surface Processes and Landforms, 30(7), 845–866. https://doi.org/10.1002/esp.1195	Model development	Spain	Mediterranean Forests, Woodlands & Scrub	Medium	Mid.	Flow regulation	Process-rule-based	Species group	Recruitment, growth, mortality, sedimentation/erosion, uprooting	Topographic, soil, groundwater regime	None

Ye, F., Chen, Q., Blanckaert, K., & Ma, J. (2013). Riparian vegetation dynamics: Insight provided by a process-based model, a statistical model and field data. Ecohydrology, 6(4), 567–585. https://doi.org/10.1002/eco.1348	Model develop-ment	China	Tropical & Subtropical Moist Broadleaf Forests	Very large	Low	Flow regulation	Process-equation-based	Species group	Recruitment, growth, mortality, competition	Topographic, flow regime	resubstitution
							Correlative (static)	Single species		Flow regime, ground water regime	resubstitution
Benjankar, R. M., Burke, M., Yager, E. M., Tonina, D., Egger, G., Rood, S. B., & Merz, N. (2014). Development of a spatially-distributed hydroecological model to simulate cottonwood seedling recruitment along rivers. Journal of Environmental Management, 145, 277–288.	Model develop-ment	USA	Temperate Conifer Forests	Large	Mid	Flow regulation	Expert-based (static)	Single species	Recruitment	Topographic, flow regime	independent
García-Arias, a., Francés, F., Morales-de la Cruz, M., Real, J., Vallés-Morán, F., Garófano-Gómez, V., & Martínez-Capel, F. (2013). Riparian evapotranspiration modelling: model description and implementation for predicting vegetation spatial distribution in semi-arid environments. Ecohydrology, n/a-n/a. https://doi.org/10.1002/eco.1387	Model develop-ment	Spain	Mediterranean Forests, Woodlands & Scrub	Medium	High	Free flowing	Process-equation-based	Species group	Growth, mortality	Soil, climate, flow regime, ground water regime	resubstitution
				Medium	Mid	Flow regulation					independent
Perona, P., Molnar, P., Savina, M., & Burlando, P. (2009). An observation-based stochastic model for sediment and vegetation dynamics in the floodplain of an Alpine braided river. Water Resources Research, 45(9), 1–13. https://doi.org/10.1029/2008WR007550	Model develop-ment	Switzerland	Temperate Broadleaf & Mixed Forests	Medium	High	Flow regulation	Process-equation-based	Species group	Recruitment, mortality	Flow regime	hold out (temp.)

Table D 2: Database of scientific publications regarding models for the distribution of riparian vegetation on reach scale. Publications belonging to the same unique model are grouped by the background color (grey/white).