Volume 27 (April 2017), 161–171

Herpetological Journal

FULL PAPER

Published by the British Herpetological Society

Environmental determinants and temporal variation of amphibian habitat use in a temperate floodplain

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The conservation of amphibians is of increasing relevance due to their ongoing and rapid decline. Alterations of floodplains are a major contributor to these declines in temperate Europe. In this study, we assessed the factors determining the abundance of four anuran species (*Rana arvalis, Pelobates fuscus, Bombina bombina* and *Hyla arborea*) in a dynamic floodplain in Central Europe during two hydrologically markedly differing years. We identified species responses to habitat characteristics using zero-inflated models. Only pond surface area explained the abundances of all species investigated in both years. Pond hydroperiod was the second most informative variable, determining site selection of all species except *R. arvalis* in both years independent from inter-annual landscape variability. Temporal variability in habitat use was determined by water chemistry and morphology of ponds in the year with frequent floods, whereas aspects of vegetation were more important in the year with the lower water level. Our results underline the importance of accounting for temporal variability of habitat use as facilitated by habitat heterogeneity in conservation planning.

Key words: amphibians, flood plains, habitat models, landscape dynamics, temporal variability, zero-inflated models

INTRODUCTION

The global loss of biodiversity is mainly caused by habitat loss and degradation (Millennium Ecosystem Assessment, 2005). Deteriorating habitat conditions can often be attributed to changes in land use and the direct or indirect effects of climate change. As a consequence, the improvement of degraded habitats is an important task in nature conservation (EC, 2011; Villard & Metzger, 2014).

Dynamic landscapes are among the most severely impacted ecosystems. In densely inhabited regions, such as Central Europe, up to 90% of floodplains are degraded, and devoid of natural water level dynamics due to river regulations and flood protection (Tockner et al., 2008; EEA, 2016). In addition to direct human impacts from land use, the hydrological conditions in European floodplains are predicted to be increasingly affected by climate change, leading to extreme floods and droughts alongside shorter hydroperiods (Hall et al., 2014; IPCC, 2014). The joint effects of local human impacts and climate change result in a major loss of habitats for amphibians, and contribute considerably to their decline in Europe (Temple & Cox, 2009). Globally, amphibians face the most rapid declines among major taxonomic groups (Blaustein et al., 2010; Henle et al., 2010; Capon et al., 2013; Meredith et al., 2016). Effective conservation necessitates sufficient understanding of species-habitat interactions across spatial and temporal scales.

Dynamic landscapes are characterised by the continuous destruction and creation of suitable habitat patches (e.g. Johst et al., 2011) and their availability for specific life stages may differ among years (Jakob et al., 2003; Balzan, 2012). Accordingly, species in dynamic landscapes typically exhibit a pronounced flexibility in habitat use (Cain et al., 2008; Ilg et al., 2008; Ayllón et al., 2014; Uboni et al., 2015). In dynamic floodplains, a large number of heterogeneous ponds occur after stochastic floods and dry out during the summer months (e.g. Ward & Stanford, 1995; Junk, 1999; Tockner et al., 2010). Species depending on the annually changing availability of freshwater patches are spatially structured among ponds of different hydroperiods (invertebrates: Lytle & Poff, 2004; Henle et al., 2006a; pond-breeding amphibians: Wellborn et al., 1996; Jedrzejewska et al., 2002; Jakob et al., 2003; Richter-Boix et al., 2006; Hartel et al., 2011). For aquatic larvae of pond-breeding amphibians, successful development highly depends on a sufficiently long hydroperiod to reach metamorphosis (Griffiths, 1997; Wellborn et al., 1996; Lane & Mahony, 2002).

Despite the risk of pond drying, pond-breeding amphibians in Europe may occur in species-rich communities in generally dynamic wetlands (Real et al.,

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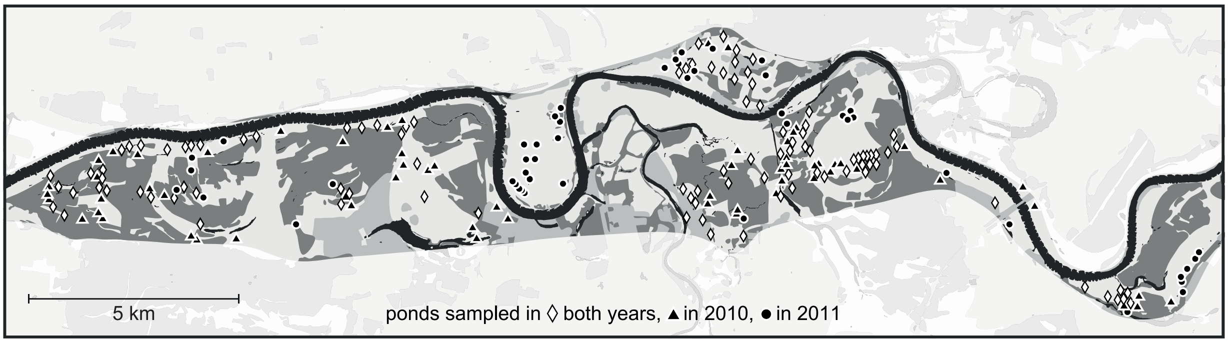

Fig. 1. Map of the study area in the middle Elbe River floodplain (51°51.500' N; 12°12.316' E), illustrating the patchy mosaic of the main landscape characteristics; black: water, dark grey: forested areas, medium grey: agriculture and human settlements, light grey: meadows, black dots: water bodies sampled in the first or the second year or in both years, light area: landscape surrounding the study area.

1993; Jedrzejewska et al., 2002) and temperate river floodplains (Morand & Joly, 1995; Henning & Schirato, 2006; Tockner et al., 2006). While spawning site selection is critical, there is however still little understanding about how species detect ponds with suitable hydroperiods (Tockner et al., 2006; Gómez-Rodríguez et al., 2009). Taking into account the temporal variability of habitat use might improve predictive models of amphibian distribution to make conservation and management efforts more effective.

The purpose of this study is to investigate the habitat characteristics that determine spawning site selection and the abundance of four amphibian species in a semi-natural floodplain in Central Europe. Each species investigated represents a different reproductive strategy typical for temperate pond-breeding amphibians. The earliest breeding species in spring is the moor frog (*Rana arvalis*), an explosive breeder with fast-developing tadpoles (Glandt, 2006). The spadefoot toad (*Pelobates fuscus*) has an extended reproductive period which can last for 2-3 months, and a larval development ranging from 3 to 13 months (Nyström et al., 2002). The European tree frog (*Hyla arborea*) and the fire-bellied toad (*Bombina bombina*) are prolonged breeders which produce multiple clutches during summer, when pond drying becomes a major threat for larvae (Vorndran et al., 2002; Glandt, 2004). Our hypothesis is that, while the hydroperiod is the major driver of species distribution in the floodplain, the study species respond differently to hydroperiod and pond characteristics. We further expect the species-specifc responses to habitat characteristics to differ between years.

METHODS

Study area

Our study took place in the floodplain of the Middle Elbe Reserve, Germany, part of the UNESCO Biosphere Reserve "Elbe River Landscape" (Scholten et al., 2005). The study area was approximately 22 km × 4 km in size and mainly located on the southern side of the Middle Elbe River (Fig. 1). The landscape is characterised by hardwood floodplain woodland (total cover: 60.1%) and open grassland used as extensive pasture (38.5%). Anthropogenic structures (1.4%) include settlements, arable land and roads.

Data collection

During surveys in 2010 and 2011 we sampled 204 floodplain water bodies located in open grassland (63.4%), at forest borders (23.1%), and within the riverine forest (13.4%). The two years of data collection differed in hydrological conditions (WSV/BfG, 2011) and consequently, only 99 of the water bodies could be sampled in both years. The four studied anuran species (*R. arvalis*, *P. fuscus, B. bombina, H. arborea*) are nationally classified as threatened, but locally still occur in high densities (Manzke & Scholz, 2004; Meyer et al., 2004; Kühnel et al., 2009).

We accounted for different activity periods by visiting the sampling sites at different times of day and night (Schlüpmann & Kupfer, 2009, Table 1). We started data collection with the first observed *R. arvalis* male, and conducted four surveys (3 days, 1 night) during the week of reproductive activities of this species. After that week, we visited each pond at intervals of about ten days (14 times in total) from March to July. The calling activity of *P. fuscus* started in the same week as *R. arvalis* and could be detected during five surveys. From April until mid-June (Table 1) four nocturnal surveys were carried out for *H. arborea.* Calling individuals of *B. bombina* could be documented over the entire survey period in the daytime as well as at night, resulting in eleven sampling dates in 2010 and seven in 2011.

While *R. arvalis* was mainly surveyed visually, the remaining species were recorded acoustically. For *P. fuscus* and *B. bombina* the counting of single males was possible, whilst for *H. arborea* abundance categories of 50 individuals were used. We eliminated any ties by drawing a random number for each data point from the range of abundances covered by the class. We only included the maximum abundance observed in the main breeding periods for statistical analyses (following Pellet et al., 2007). Sites were always approached from the same access point, although the actual point of observation could change due to pond drying. We approached the sites on foot and allowed a recovery period of 10 minutes to reduce disturbance. We selected

41 environmental variables based on literature to explain the abundance and distribution of the four species (Table 2). We measured variables of pond morphology, such as the bank slope and vegetation cover at the beginning (March) and the end (July) of the survey and used mean values for analyses.

Vegetation cover was estimated visually on three scales: inside the pond, at the bank, and in a buffer 50 m around each pond. We measured variables that vary temporally repeatedly and simultaneously with the species surveys over the entire study period. To describe the influence of floods on each pond, we used connectivity as a categorical parameter (directly flooded, connected to the river by channels, or not directly connected). We measured water chemistry for each pond (pH, oxygen concentration, and conductivity) on three different dates: during the first surveys when the temporary ponds were filled, when the ponds were full, and on a third occasion shortly before it dried out (measurement device: Multi 350i, WTW; electrodes: CellOx 325 WTW, TetraCon 325 WTW, SenTix 41-3 WTW). We included the presence of predatory species, such as fish or carnivore insects, observed during the survey or by dip netting.

Statistical analyses

To identify environmental variables that influence the abundances of the four anuran species, we analysed data separately for each species and each year. Count data of all species in both years were zero-inflated and consequently, we used zero-inflated mixed models (ZI models). ZI-models contain two components, one accounting for occupancy (including the probability of imperfect species detectability) and another one that evaluates abundances given that a site is occupied (e.g., Zuur et al., 2009). We reduced the number of variables before analysing the data with ZI-models separately for the two parts of the ZI-models in three steps (see Fig. 2). Firstly, we used a non-parametric hierarchical clustering approach (Harrell, 2013) to identify variables that correlated with a Spearman-correlation coefficient higher than 0.5. If this was the case, we excluded the variable with the more uneven distribution and thus less continuous information quality. In the next step, we determined the relative importance of the non-correlated variables by employing a conditional random forest (*cforest*) approach (Strobl et al., 2009) and developed regression and classification trees for count data and occupancy data, respectively. For model fit, we tested the default values suggested by Liaw & Wiener (2002) against lower numbers of variables per node and higher numbers of trees. Model selection based on the AUC-values (Area Under the Curve; Fielding & Bell, 1997) and variables with a relative importance value > 0 were retained.

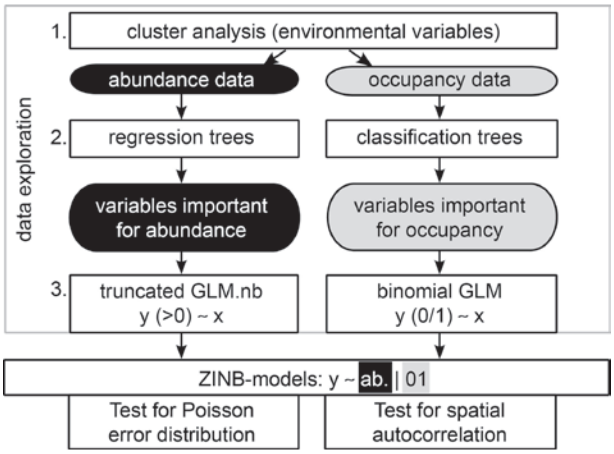

Fig. 2. Workflow scheme of the variable pre-selection procedure and the ZI-habitat models, conducted for each species and each year separately: 1. cluster analysis (eliminating correlations), 2. Regression trees with count data and classification trees with occupancy data (identifying relative variable importance), and 3. GLMs (identifying the significances of variables, variable interactions and power-functions). Remaining variables were summarised in zero-inflated models that assumed a negative binomial distribution of counts (ZINB).

In a third step of the procedure to reduce variables, we tested retained variables in GLM-models (generalised linear regression models, McCullagh & Nelder, 1989) to identify any significances in variables, interactions, and power functions. For the variables retained from the regression trees (count data), we conducted truncated GLM-models with a negative binomial error distribution, whereas the variables that were retained from the classification trees (occupancy data) were analysed with GLM-models with binomial error distribution (e.g. Venables & Ripley, 2002). Significant variables, power functions and interactions were retained for the analysis of the two components in the ZI-models. For ZI-models negative binominal (ZINB) or Poisson (ZIP) error distribution might be appropriate (e.g., Martin et al., 2005; Dénes et al., 2015). Therefore, we tested both possibilities and selected the model with the lowest AIC-value (Akaike's information criterion; Akaike, 1974) as the habitat model. We then tested each of the eight habitat models selected (one for each of the four species in both years) for spatial autocorrelation of model residuals by calculating Moran's I (Cliff & Ord, 1981). In the case of spatial autocorrelation, we included a residual autocovariate in the ZI-model (Online Appendix 1) as suggested by Crase et al., (2012).

All analyses were carried out using the program R, version 2.15.0 (R-Core-Team, 2013, see Online Appendix 1 for R-packages and functions used). For the interpretation of our results in an ecological context, we present the functional relationships between the abundances predicted by the ZI-models and the single measured environmental variables.

RESULTS

Inter-annual variability of the landscape and the species investigated

The two-year study was characterised by high inter-annual variability in hydrological conditions (WSV/BfG, 2011). In addition to the regular spring flood in March, a second flood took place in April during the first year

Table 1. Details of the amphibian surveys: Dates of the survey (first line), dates of spawning, number of occupied sites, and mean maximum abundance of calling males per site. * Survey dates may differ by 1-2 days due to suitable/unsuitable weather conditions

Survey dates (both years)*	22.03., 26.03., 02.04., 08.04., 17.04., 28.04., 05.05., 15.05., 26.05., 07.06., 14.06., 28.06., 09.07., 13.07.			
Species	Year	Spawning-period	Occupied sites	Mean number of calling/observed males per site ± SE
Rana arvalis	2010	24 March – 02 April	45	134 ± 141.4
	2011	06 April – 10 April	46	88.5 ± 95.3
Pelobates fuscus	2010	25 March – 28 April	44	4.0 ± 4.2
	2011	23 March – 28 April	58	4.4 ± 4.6
Bombina bombina	2010	20 March – 13 July	60	8.3 ± 8.6
	2011	23 March – 08 May	42	7.4 ± 9.8
Hyla arborea	2010	28 April – 13 June	39	52.7 ± 29.6
	2011	15 April – 15 June	23	26.6 ± 26.3

of our study (2010), resulting in many water bodies that persisted over the entire data collection period. The second year (2011) was characterised by dry conditions, due to a winter flood between January and mid-February, with no further spring flood taking place (Fig. 3). As a consequence, the number and locations of temporary water bodies differed between the two years. We sampled 160 ponds in 2010 and 147 in 2011, 99 of which (88 temporary ponds) were identical between years. In both years, all four species co-occurred in ten (2010) and seven (2011) water bodies; in 38 (2010) and 30 (2011) ponds, only a single species occurred. In 83 (2010) and in 65 (2011) water bodies that were surveyed, no study species could be recorded. Consequently, count data of all species were zero-inflated in both years. Whilst abundance of *P. fuscus* was low in both years, abundances of the other three species were lower in 2011 when the duration of calling activity of *R. arvalis* and *B. bombina* was shorter compared to 2010 (Table 1).

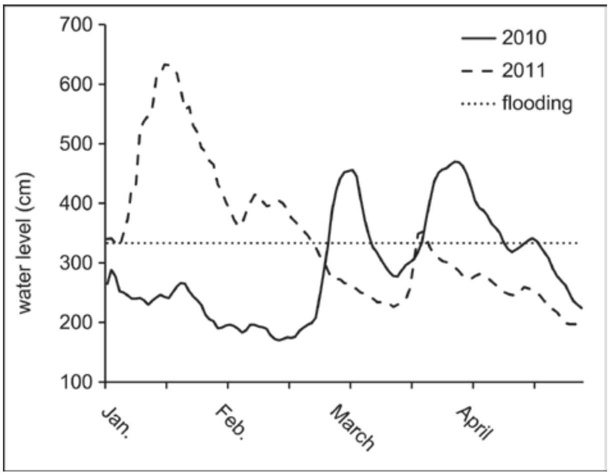

Fig. 3. Fluctuations of the Elbe River water level in the study area over the two years of data collection; the dotted line indicates the flooding threshold. Source: WSV/BfG (2011).

Main determinants of amphibian abundances at spawning sites

All models generated robust results, and the ZI-habitat models were conducted with negative binomial error distribution (AUC- and AIC-values are given in Online Appendix 2A,B). Of the 41 variables listed in Table 2, nine had to be excluded due to their high correlation with other factors or low data quality (Online Appendix 3). The pre-selection using cforest trees and GLM-models further reduced the variable set to between eight and 13 variables. Variable interactions and power functions that were analysed in the ZINB-models are given in Online Appendix 4. The significant functional relationships of the single variables with species abundances are summarised in Table 3 (see Online Appendix 4 for complete model results).

Of the 28 factors retained, 23 had significant influence on the abundances of at least one of the four study species (Table 3). Two factors related to hydrodynamics (surface area and hydroperiod of ponds) were major determinants in both years. Species abundances predicted by the ZINB-models of all four species were always positively correlated with pond surface area, whilst the pond hydroperiod determined the abundances of *H. arborea* only in the wet year (Fig. 4), and had no influence on the abundance of *R. arvalis*. In addition to the overall positive relationship between the hydroperiod and species abundances, only *B. bombina* showed an increased abundance at ponds with an intermediate length of the hydroperiod in the wet year.

Temporal variability in habitat use

In 2010, water chemistry and morphology had a stronger influence on species abundances than in 2011, when aspects of vegetation cover dominated. In the wet year all species obtained the highest abundance at an intermediate pH-value (pH) of about 7.3. In the dry year, however, only the abundance of *R. arvalis* was influenced by pH. Likewise, water conductivity (Cond) influenced the abundances of *R. arvalis* and *H. arborea*, having been

Table 2. List of names, abbreviations, units, and ranges of the environmental variables sampled in the study area; median-values displaying landscape variability between the two years of the study.

			2010		2011	
Category/Name	Abbreviation	unit	median	mean ± SE	median	mean ± SE
Water chemistry						
Oxygen	O_2	mg/l	5.6	6.1 ± 2.6	7.8	8.2 ± 3.0
pH	pH	pH	7.3	7.3 ± 0.4	7.6	7.7 ± 0.5
Conductivity	Cond	µS/cm	453.4	517.8 ± 240.0	382.0	445.9 ± 233.5
Water temperature						
March	TeM	°C	7.2	7.2 ± 1.7	5.2	5.5 ± 1.7
April	TeA	°C	7.6	7.9 ± 1.7	9.8	10.2 ± 1.8
Shallow water zones (< 20 cm) and their variation during pond desiccation						
Percentage	Sh	%	33.1	43.4 ± 35.5	37.1	41.0 ± 25.7
Variation	DSh	%	25.0	40.0 ± 37.5	80.0	64.2 ± 35.5
Distributed all-over	Sh1	%	50.0	51.6 ± 31.3	50.0	47.5 ± 28.9
Distributed at one side	Sh2	%	12.5	19.7 ± 23.8	16.7	19.8 ± 19.8
Distr. at several sides	Sh3	%	0.0	4.7 ± 9.8	0.0	12.8 ± 18.0
Variation of these distr.	DsT	ordinal	2.0	2.2 ± 0.9	3.0	2.6 ± 0.9
Flooding						
Connection to the river	Conn	ordinal	2.0	2.1 ± 0.9	3.0	2.3 ± 0.8
Pond permanency						
Hydroperiod	Hydro	weeks	12.5	15.4 ± 7.1	10.0	12.0 ± 7.8
Structural factors of the water body						
Bank slope	BaS	%	27.8	29.7 ± 21.3	25.0	24.9 ± 16.3
Exposure to sunlight	Sun	%	75.0	64.0 ± 33.6	82.5	70.6 ± 29.8
Surface area	Size	m²	732.4	2893.8 ±8510.5	358.3	3157.6 ±16226.8
Dynamic of size	DyS	%	100.0	90.8 ± 24.3	100.0	96.1 ± 16.5
Depth of ground	DeG	cm	2.6	3.0 ± 1.8	3.8	4.6 ± 2.7
Grain size at ground	SoG	mm	2.0	2.6 ± 1.3	2.0	2.5 ± 0.9
Grain size at bank	SoB	mm	4.0	4.0 ± 1.3	4.0	4.0 ± 1.2
Biological factors						
Presence of predators	Pred	binomial	1.0	0.5 ± 0.5	0.0	0.4 ± 0.5
Vegetation cover within the water body						
Algae	WaA	%	0.0	2.6 ± 10.0	0.0	2.7 ± 6.7
Carpets of grasses	CaG	%	0.0	12.9 ± 22.6	5.0	9.4 ± 11.6
Submerged herbs	Sub	%	0.0	3.0 ± 10.5	2.5	6.9 ± 12.7
Vertical structures	Vert	%	5.0	13.5 ± 17.3	7.5	11.9 ± 12.9
Matured wood	MaW	%	0.0	1.0 ± 4.7	0.0	5.8 ± 8.7
None	NoSu	%	0.0	6.8 ± 14.7	15.0	20.9 ± 21.0
Vegetation cover at the water's edge						
Grassy vegetation	GrB	%	21.9	24.2 ± 20.4	45.0	44.6 ± 26.1
Herbaceous vegetation	HeB	%	6.3	7.8 ± 6.5	12.5	13.8 ± 8.3
Stinging nettles	StB	%	0.0	9.5 ± 17.0	0.0	1.6 ± 3.9
Reed	ReB	%	0.0	11.2 ± 16.1	0.0	6.3 ± 13.9
Leafs	LeB	%	0.0	5.1 ± 11.8	2.5	6.1 ± 10.0
No vegetation	NoB	%	0.0	4.9 ± 10.4	5.0	13.7 ± 13.9
Woody vegetation	WoB	%	2.5	5.5 ± 7.8	10.0	8.8 ± 11.4
Vegetation cover of the surrounding (up to 50 m)						
Grassy vegetation	GrS	%	39.6	39.7 ± 24.3	45.0	43.1 ± 22.5
Herbaceous vegetation	HeS	%	15.8	17.0 ± 8.5	17.5	17.9 ± 8.3
Stinging nettles	StS	%	5.0	11.8 ± 17.7	2.5	5.1 ± 8.9
Leafs	LeS	%	1.7	6.7 ± 10.8	2.5	3.4 ± 5.0
Without vegetation	NoS	%	0.0	1.6 ± 4.1	2.5	4.0 ± 6.4
Woody structures	WoS	%	17.1	22.5 ± 21.7	15.0	19.8 ± 15.4
Height of vegetation	HeV	cm	36.0	41.0 ± 27.3	25.5	28.6 ± 13.0

highest in water bodies with a conductivity of about 500 µS/cm in the wet year, whereas in the dry year it had no effect on abundance. Similarly, *R. arvalis* and *P. fuscus* reached highest abundances at water bodies with a low oxygen concentration (O_2) in the wet year, whereas in the drier year abundances of both species were independent of oxygen.

The abundances of two species (*P. fuscus* and *H. arborea*) were highest at an intermediate depth of loose ground soil (DeG) in 2010, whereas abundance was generally independent of DeG in 2011. *Rana arvalis* and *B. bombina* reached highest abundances at water bodies with a bank slope below the median value, whereas in 2011 abundance again was generally independent of slope. In 2010, *H. arborea* reached highest abundance at directly flooded ponds (Conn), whereas in 2011, *R. arvalis* reached highest abundances at ponds whose water levels were affected by ground water or a channel connection, but not directly flooded.

Variables related to vegetation structure were primarily important in the drier year, with the percentage of bare ground at the water's edge being an exception. Exposure to sun and percentage of grass carpets in the ponds (CaG) correlated with the abundance of three species. Abundances (except for *R. arvalis*) were highest at ponds with 70% exposure to sun but only for *H.*

Table 3. Overview of the environmental variables analysed in the eight ZINB habitat models for four species and two years separately; variables remaining from the pre-selection procedure and thus implemented in the ZINB-models are marked with X in the columns "*ZI-analysed*"; significant functional relationships ("*func. relat.*) of species abundances and the measured variable are presented either with the parameter values for maximum abundance (in case of power functions) or by positive (+) or negative (–) functional relationships. The first column contains the abbreviation of the variable, see Table 2 for full names, and see Appendix 4 for variable interactions and power functions. (AC: the residual autocovariates that have been implemented in models with spatial autocorrelation in residuals).

Species	*Rana arvalis*				*Pelobates fuscus*				*Bombina bombina*				*Hyla arborea*			
Variable	ZI-analysed		func. relat.		ZI-analysed		func. relat.		ZI-analysed		func. relat.		ZI-analysed		func. relat.	
	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
Habitat-structures that influenced abundance of more than one species independent of inter-annual landscape variability																
Size	X	X	(+)	(+)	X	X	(+)		X	X	(+)	(+)	X	X		(+)
Hydro					X	X	>12	(+)	X	X	13	(+)		X		
(+)																
Habitat-structures that influenced abundance of more than one species depending on inter-annual landscape variability																
a) Variables of water chemistry and pond morphology that were mainly relevant in the wetter year																
pH	X	X	7.2-7.7	>7.9	X		7.2-7.4		X	X	7.2-7.4		X		7.2-7.4	
Cond	X		500			X				X		(-)	X		400-1000	
O_2	X		(-)		X	X	4-5						X			
DeG					X		2-3		X				X		2-5	
BaS	X	X	20	(-)					X		20					
Conn	X	X		(-)									X		2	
b1) Vegetation cover mainly relevant in the dryer year																
ReB	X	X	(+)	(+)						X						
Sun						X		70	X	X		70	X	X	70	70
CaG		X		(+)		X		15		X		15				
GrB					X		10-20			X		30-60				
GrS		X		25	X		(-)			X		45				
WoS										X		>30		X		30-50
Sub						X		10-40						X		10-40
b2) Vegetation cover mainly relevant in the wetter year																
NoB		X			X		10-20		X		>10			X		10
SoG									X		2		X		(-)	

arborea sun exposure was also relevant in the wetter year. However, shallow water zones covered by CaG were mainly available in the dry year (median in the wet year: 0% and in the dry year: 5%). Whilst the abundance of *R. arvalis* was positively related to CaG, the abundance of *B. bombina* and *P. fuscus* decreased above a CaG cover of 15%. Similarly, the predicted abundance of these three species was highest when 10% of the water's edge was not covered by vegetation (NoB), which was available at fewer ponds in 2010 (median: 0%) compared to 2011 (median: 5%).

Three further variables, grassy vegetation cover of the surrounding area (GrS), percentage of woody structures in the surrounding area (WoS) and percentage of bare ground at the water's edge (NoB) were associated with the abundance of two species in the drier year. The abundances of *R. arvalis* and *B. bomina* were highest at intermediate GrS values (25% and 30-60%, respectively), and GrS was negatively correlated with the abundance of *P. fuscus* in 2010. The abundances of *B. bomina* and *H. arborea* were highest at ponds with intermediate values of woody structures (>30% and 30-50%, respectively). The positive relationship between the presence of predators and the abundance of *H. arborea* and *P. fuscus* is likely spurious (standardised dip-netting was not possible due to dense vegetation in the summer).

DISCUSSION

Dynamic landscapes are characterised by continuous changes in environmental conditions which influence habitat use at different spatial and temporal scales (Robinson et al., 2002; Ilg et al., 2008; Ayllón et al., 2014). However, temporal variability in species-habitat interactions is still insufficiently understood (Tockner et al., 2006; Gómez-Rodríguez et al., 2009). Therefore, we investigated the habitat use and determinants of abundance for four anuran species in a dynamic floodplain in Central Europe. The two years analysed differed strongly in hydrological conditions, and only pond surface area was consistently relevant for all species. Pond hydroperiod, expected to be a major driver of amphibian distribution in dynamic wetlands, was the second most relevant variable, and no other variable appeared to determine the abundances of all four species throughout the study. Responses to habitat characteristics were often species-specific, and also differed between years.

We conducted a standardised survey of calling males, a widely used method to estimate amphibian abundances (e.g. Crouch & Paton, 2002; Pillsbury & Miller, 2008). However, even with standardised data collection and analysis, differences in species abundance measures as well as in environmental data can be high, especially true for temporary sampling sites such as floodplain pools (MacKenzie et al., 2002; Henle et al., 2006b; Pellet et al., 2007). We nevertheless argue that the direct comparison of standardised methods enabled a comparison of the dynamics of habitats and their effects on species abundances in our case.

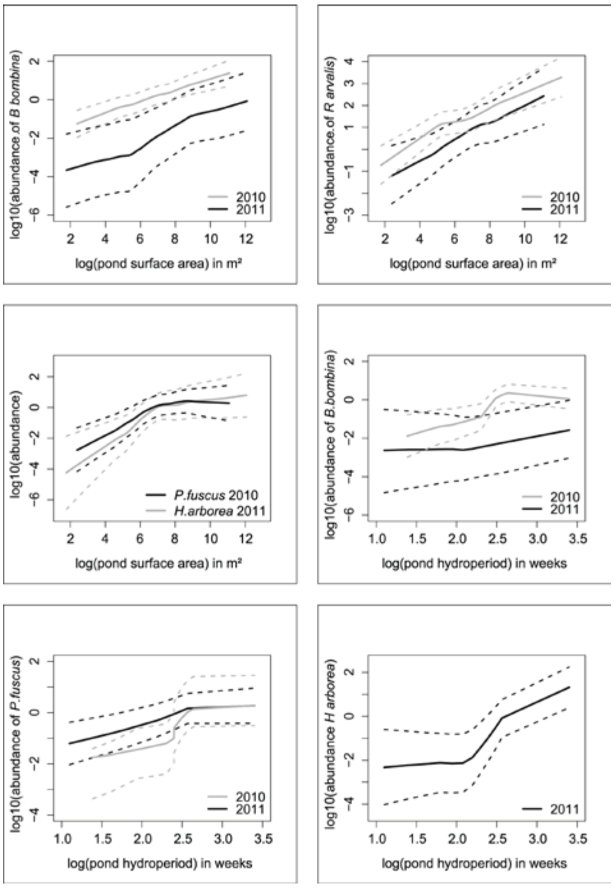

Fig. 4. Functional relationships between species abundance and the measured values of the pond's surface area (upper three graphs) and the hydroperiod (lower three graphs); dotted lines show 95% confidence intervals.

The relationship between pond surface area, hydroperiod, and amphibian abundances

Our results showed an overall positive relationship between the abundance and pond surface area and hydroperiod, indicating that the study species preferred larger, more stable ponds. Nevertheless, most preferred sites were highly dynamic in terms of surface area, and 80% of all sampled sites were temporary in the drier year of the study. Babbitt (2005) found a stronger impact of pond surface area on amphibian distribution in dynamic wetlands compared to in less dynamic habitats. Similarly, whereas the hydroperiod determined the distribution of *H. arborea* in dynamic wetlands (Edenhamn 1996; Hartel et al., 2011), it had no influence in a less dynamic cultural landscape (Van Buskirk, 2005). Likewise, a preference of *R. arvalis* and *P. fuscus* for temporary or permanent ponds is controversial (Nyström et al., 2002; Glandt, 2006; Loman & Andersson, 2007). Only *B. bombina* has been shown to have a consistent dependence on temporary ponds (e.g., Nicoara & Nicoara, 2007).

Our results further exemplify the interaction of hydrological variability in dynamic wetlands and temporal segregation of species with different reproduction strategies. *Rana arvalis* was not influenced by hydroperiod, which might be explained by its early spawning time and short larval development (Glandt, 2006). *Pelobates fuscus* also starts its reproduction early, but requires longer for larval development (Nöllert, 1990) and consequently is affected more by pond drying. The latest spawning species, *H. arborea,* was first recorded when several ponds had already dried out, explaining the preference for more permanent ponds. Only *B. bombina* showed highest abundances at ponds with an intermediate hydroperiod in 2010, confirming its preference for temporary ponds (Nicoara & Nicoara, 2007). In 2011, abundance correlated positively with hydroperiod and is likely a response to higher desiccation risk in drier years.

Temporal variability in microhabitats and amphibian habitat use in a floodplain

The analyses of two hydrologically different years enabled us to quantify temporal differences in environmental variables which explain the abundance of species. Water chemistry and morphology had a greater influence on abundance in the wet year compared to the dry year, when aspects of vegetation cover were more important. In 2010, two spring floods connected some of the study ponds with the river. Flooding of ponds affects their morphology and water chemistry (e.g., Ward & Stanford 1995, Weigelhofer et al., 2014). However, the chemistry of water sources vary among rivers as well as among floodplains along the same river (e.g., Arscott et al., 2000; Cushing et al., 2006). The measured pH values in both years were within the tolerance levels for the studied species (Nöllert, 1990; Glandt, 2004; Nicoara & Nicoara, 2007; Jędrzejewska et al., 2003), and the occurrence of highest abundances at median pH levels likely was due to such values being most common in the environment.

We observed a shift in importance towards variables related to vegetation cover in the drier year. For floodplain specialists, succession reduces habitat suitability (Grimm et al., 1994; Schludermann & Spolwind, 2001), while disturbance caused by floods resets succession to early stages (e.g., Ward & Stanford, 1995; Amoros & Bornette, 2002). A higher relevance of wooden structures surrounding ponds for *H. arborea* and *B. bombina* in 2011 indicates that shelter provided by woody structures is less relevant in wet years. Availability of daytime cover to protect against water loss allows amphibians to reach higher abundances (e.g., Dupuis et al., 1995). Another example for inter-annual differences was that the importance of shallow water zones with carpets of dead grasses in the dry but not the wet year. These carpets created small islands, which were important microhabitats for *B. bombina*, *P. fuscus*, and particularly for the early-breeding *R. arvalis*. Likewise, the percentage of bare ground at the water edge was relevant in 2011 but not in 2010 for all species. This may, however, be a consequence of few ponds having such sections in the wet year. Overall, our results corroborate previous findings on the temporal variability of habitat use of amphibians in dynamic wetlands (Jakob et al., 2003; Richter-Boix et al., 2006; Gómez-Rodríguez et al., 2009; Hartel et al., 2011). Temporal variability in habitat use is also common in other taxonomic groups in which habitat characteristics change over time (Ilg et al., 2008; Ayllón et al., 2014; Uboni et al., 2015).

Consequences of inter-annual variability in amphibian site selection for conservation planning in temperate floodplains under the aspect of climate change

Amphibians are generally vulnerable to the effects of climate change because of their limited dispersal ability (Araújo & Pearson, 2005; Henle et al., 2010; Meredith et al., 2016). Therefore, in addition to providing suitable microhabitats, floodplains that are able to function as dispersal corridors are an important aspect for amphibian conservation, especially in temperate and fragmented regions (Henning & Schirato, 2006; Tockner et al., 2006; Henle et al., 2010). However, suitable habitat heterogeneity in floodplains requires their ecological functionality, including a full range of discharges ranging from low flows to flood regimes with different magnitudes, frequency, and duration (EEA, 2016). However, dynamic floodplains have already lost much of their functionality due to human land use (Tockner et al., 2008; EEA, 2016), which is increasingly exacerbated by climate change. Local consequences of climate warming predict an increase in temperature coupled with a reduced hydroperiod (Carey & Alexander, 2003; Blaustein et al., 2010), and heterogeneous wetlands are among the landscapes most at risk (Capon et al., 2013; IPCC, 2014). The re-naturalisation of the hydrological dynamics in European floodplains is a core component in recent efforts of sustainable flood prevention, aiming to re-connect the retention areas of floodplains to rivers (Schindler et al., 2014; EEA, 2016). Effective amphibian conservation in Central Europe can be realised as part of the efforts towards protecting humans and their assets against extreme floods. Our results contribute to the improvement of predictive models of amphibian distribution in floodplains that can be used to make floodplain restoration and management efforts more effective.

ACKNOWLEDGEMENTS

Great thanks go to K. Enders and F. Schildhauer for assistance in the field. D. Dick received financial support from the German Foundation for the Environment, DBU (Deutsche Bundesstiftung Umwelt). Furthermore, this work was kindly supported by the Helmholtz Impulse and Networking Fund through the Helmholtz Interdisciplinary Graduate School for Environmental Research (HIGRADE, Bissinger & Kolditz, 2008). We would also like to thank S. Lampa, C. Schulz-Zunkel, A. Grimm, and anonymous reviewers for constructive suggestions.

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Accepted: August 26th 2016

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