Differential response to abiotic conditions and predation risk rather than competition avoidance determine breeding site selection by anurans

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Co-existence of species has been a central debate in ecology for decades but the mechanisms that allow co-existence are still heatedly disputed. The main paradigms have shifted among the importance of competition, predation and abiotic conditions as determinants of community structure. Differential habitat selection is considered to reduce competition and hence allow co-existence. Our goal was to test hypotheses regarding how breeding site use of a population that was patchily distributed on a dynamic floodplain may facilitate coexistence: 1) do species co-occur randomly or do they occur more or less often than expected by chance? 2) Do species use the same habitat types in equal proportions or do they use them differentially? 3) If they use habitat types differentially, is this differential use related to abiotic and biotic conditions? 4) Does interspecific competition predict breeding site use or do abiotic conditions and predation risk better predict habitat use? We collected presence/absence (i.e. detection/nondetection) data of egg clutches and larvae of four pond-breeding anuran species during a two year study at a total of 353 ponds. We used site occupancy models and model averaging techniques to predict breeding site selection in relation to habitat types, abiotic and biotic factors. These parameters were corrected for imperfect detection of species. The rates of co-occurrence were consistently higher than expected by chance. Species differed in the use of the main habitat types. Habitat types that were used by multiple species were used in a species-specific manner in relation to both abiotic conditions and predation risk. Species preferred ponds where other species and fish were present. Although niche differentiation in breeding site selection is evident, our results do not support the pervasive role of competition avoidance in governing current breeding site selection. We conclude that differential habitat use and differences in response to abiotic conditions and predation risk can override competitive interactions, thereby facilitating local co-existence and high species diversity.

Identifying the factors that promote co-existence of species has been a central debate in ecology for decades (Gause 1934, Hutchinson 1959, Pianka 1967, Hairston 1980, Levine and HilleRisLambers 2009). The main controversy has been on the importance of biotic vs abiotic processes in controlling the local and regional co-existence of species. For example, do competitive interactions exclude species from their potential ranges (Gause 1934, Hardin 1960), or are species ranges more affected by predation risk (Menge and Sutherland 1976, Gallet et al. 2007)? Abiotic con-straints surely limit the distribution patterns of species (Connell 1978, Dunson and Travis 1991), but how important are abiotic factors at the local scale? In attempts to explain distribution patterns across large regions some success has even been made by assuming that all species are

ecologically equivalent (e.g. "neutral") (Hubbell 2001, Muneepeerakul et al. 2008). We postulate that most biotic and abiotic processes that determine co-existence of species occur at local scales, i.e. within- and among those habitat patches that are within the range of individual habitat choice (Enright et al. 2007). We explored whether amphibian species differentially select breeding sites in relation to both abiotic and biotic factors, which would facilitate local co-existence (Levine and HilleRisLambers 2009).

The maternal selection of breeding site is a crucial step in the complex life cycle of pond-breeding amphibians as it sets the scene for larval development, which in turn affects survival and fitness in the terrestrial stage (Smith 1987, Berven 1990, Rieger et al. 2004). The emerging view of

studies focusing on breeding site selection is that abiotic and biotic conditions (mainly predation risk) jointly affect breeding site selection (Laurila 2000, Knapp et al. 2003, Resetarits 2005, Van Buskirk 2005, Richter-Boix et al. 2007, Binckley and Resetarits 2008). Among biotic factors, the role of interspecific competition in breeding site selection, however, may still be underappreciated (but see Resetarits and Wilbur 1989, Van Buskirk 2005). This is surprising, as for example competition for food is usually strong in larval communities; and there is consensus about the negative impacts of strong competition on larval performance (Wilbur 1977, Semlitsch 1987, Morin and Johnson 1988). Hence, to understand the mechanisms underlying the co-existence of species, the direct effects of competitors, predators, and the abiotic environment on breeding site selection must be clarified.

We quantified the separate and combined impacts of abiotic and biotic factors on breeding site selection by four anuran species occurring in a pristine dynamic floodplain. Breeding ponds were patchily distributed on the riparian forest and on the open active tract. The active tract is frequently reworked by floods, thereby counteracting succession and the establishment of predators. Ponds in the active tract have therefore more variable hydroperiod, contain fewer predators and are warmer than ponds in the riparian forest (Indermaur 2008). As all species could easily access all ponds along these environmental gradients, we were able to explore whether differential response to abiotic and biotic factors facilitated co-existence of species. Abiotic factors included habitat type, pond surface area, water depth, availability of structural elements for egg attachment, pH, and temperature. The biotic environment included predation risk, the presence of fish and competitors.

Our goal was to test hypotheses regarding how breeding site use may facilitate coexistence: 1) do species co-occur randomly or do they occur more or less often than expected by chance? 2) Do species use the same habitat types in equal proportions or do they use them differentially? 3) If they use habitat types differentially, is this differential use related to abiotic and biotic conditions? 4) Does interspecific competition predict breeding site use or do abiotic conditions and predation risk better predict habitat use?

Materials and methods

Study site

The study was conducted from 1 February until 30 July, in 2005 and in 2006, in an island-braided floodplain along the 7th order Tagliamento River in northeastern Italy (46°N, 12°30′E). The Tagliamento (catchment area: 2580 km²) originates at 1000 m a.s.l. in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea. Unlike most European rivers, the river retains its essentially pristine morphological and hydrological characteristics (Tockner et al. 2003).

The study site (river-km 79.8–80.8; 135 m a.s.l.) covered a 800 m wide active tract and the adjacent riparian forest (right bank). The active tract comprised a spatio-temporally complex mosaic of vegetated islands, a braided river network and ponds, embedded within a matrix of exposed gravel sediments (Indermaur et al. 2009). Within the riparian forest (right bank), ponds are distributed along an abandoned alluvial channel. The steep hillslope of Monte Ragogna borders the left bank of the floodplain. The habitat mosaic within the study area is frequently reworked by floods with highest peaks in autumn and additional peaks during snow melt in spring (Tockner et al. 2003). This river section was chosen because both habitat heterogeneity and amphibian diversity are highest (Tockner et al. 2006).

Study species

Out of eleven species that were present in the study section, we selected the four most abundant species to estimate probabilities of occurrence and the factors that affect these probabilities: the European common toad *Bufo b. spinosus*, the green toad *B. viridis*, the European common frog *Rana temporaria*, and the Italian agile frog *R. latastei*.

Bufo b. spinosus is a ubiquitous species typically spawning in permanent natural and man-made ponds (Giacoma and Castellano 2006). *Rana temporaria* is a widespread species that is often found in cool wooded areas adjacent to running waters (Giacoma and Castellano 2006). *Rana latastei* is a characteristic lowland species that spawns in permanent forest ponds but also in temporary ponds in open areas (Giacoma and Castellano 2006). *Bufo viridis* is a pioneer species preferring ponds of early succession stages in open areas (Giacoma and Castellano 2006).

Data collection

Pond selection
353 ponds (pooled data of 2005: n = 170 and 2006: n = 183) with pond surface area ≥ 1 m² and water depth > 0.05 m were selected for the study. Backwaters were also included, and their surface water area was defined as the conjunction to side channels. Ponds were located in the riparian forest (n = 123; pooled data), at the forest edge (n = 55), which is the interface between the forest and the active tract, at the edge of vegetated islands within the active tract (n = 97), as well as in exposed gravel sediments of the active tract (n = 78).

Pond surveys
We recorded egg clutches and larvae of *B. b. spinosus*, *B. viridis*, *R. temporaria*, and *R. latastei*. Each pond was surveyed at 10-d intervals between 1 February and 30 July; 16 times in total. At each sampling date, two observers searched for egg clutches and larvae. The searching time was in proportion to pond surface area and structural complexity of the ponds. Larger ponds were waded through to improve detection. Visibility of egg clutches and tadpoles was high in general because of low turbidity.

Pond attributes
We used a set of abiotic and biotic factors to estimate probabilities of occurrence (Table 1). Abiotic factors included habitat type, mean pond surface area, water depth, availability of structural elements for egg attachment, pH,

Table 1. Factors used for predicting the probability of occurrence and detection.

Process	Factor	Explanation	Sampling interval	Measuring detail	Reference
Probability of occurrence					
	YY	Year (2005, 2006)			
Abiotic condition (factor reflecting landscape context)					
	Ht	Habitat type/spatial location (4 levels: riparian forest, edge of riparian forest, exposed gravel, island edge)			Guerry and Hunter 2002
Abiotic conditions (factors reflecting hydrogeomorphology)					
	Ar*	Pond surface area [m^2]	Monthly (4 times)	dGPS (Trimble GeoXT, Zurich)	Pearman 1993
	De*	Water depth [m]	Weekly	Maximum water depth	Pearman 1993
	St	Availability of structural elements for egg attachment: coverage by twigs, branches and aquatic vegetation [%]	Monthly (4 times)	Visually	Mazerolle et al. 2005
Abiotic condition (factors reflecting water quality)					
	pH*	pH [H$^+$]	Monthly (4 times)	WTW pH 340[†]	Cummins 1986
	T*	Mean maximum temperature °C	Hourly	Thermochron ibutton loggers DS1921G	Herreid and Kinney 1967
Biotic condition					
	Fi[†]	Fishes ≥10 cm (present/absent)	Monthly (4 times)	Visually	Knapp et al. 2003
	Pr[§]	Predation risk (index: 0-1)	Once	Sweep netting and funnel traps proportional to pond surface area	Skelly and Werner 1990, Knutson et al. 2004
	Pbb	Presence of *Bufo b. spinosus* (0,1)	Weekly	Visually	
	Pbv	Presence of *B. viridis* (0,1)	Weekly	Visually	
	Pte	Presence of *Rana temporaria* (0,1)	Weekly	Visually	
	Pla	Presence of *R. latastei* (0,1)	Weekly	Visually	
Probability of detection					
	YY	Year (2005, 2006)			
	Day*	Day in the season			
	Ar*	Pond surface area [m^2]	s. above		
	De*	Water depth [m]	s. above		
	Si	Site (two levels: riparian forest, active tract)			

See Supplementary material Appendix 2 for all factors that were measured.
[†]More than 30 species of fish are known to inhabit the Tagliamento river. In the ponds that we studied, four species were encountered most commonly: *Leuciscus cephalus*, *Alburnoides bipunctatus*, *Cottus gobio* and *Rhodeus amarus* (Indermaur unpubl.).
*Factor that were also modelled as quadratic terms to reflect non-linear responses of species to environmental factors.
[†]Wissenschaftlich-Technische Werkstätten, Weilheim, Germany.
[§]Sum of individuals of newts (*Triturus carnifex*, *T. vulgaris*), snakes (*Natrix natrix*), insects (larvae and adults of *Dytiscus marginalis*, *Aeshna* sp.), normalized between 0 and 1.

and temperature. Biotic factors included the presence of fish, predation risk, and the presence of other anuran species than of the focal species. Details on sampling intervals, measuring methods as well as the construction of the predation index are presented in Table 1. For other factors that were measured but omitted in the analyses to minimize collinearity of explanatory factors, see Supplementary material Appendix 1, 2.

Statistical analyses

Model selection
We used a model selection approach to identify appropriate statistical models for estimating probabilities of detection (p) and occurrence (ψ) (Burnham and Anderson 2002, MacKenzie et al. 2002, Schmidt 2005). We used both abiotic and biotic factors that were supported by the literature, either with linear and/or quadratic effects, to construct candidate models for p and ψ (Supplementary material Appendix 3, 4). The data were analysed in two steps. First, we estimated p per species. Second, we used

the model that best explained p to find a model that best explains ψ. We moved p-related information to Supplementary material Appendix 3–5 as p was simply estimated to correct ψ for imperfect detection.

Model fitting
For estimation of p and ψ we used the R (R Development Core Team 2005) package RMark (v1.8.0) (Laake and Rexstad 2008) to construct linear models for program MARK (White and Burnham 1999). All continuous explanatory factors were z-standardized prior to analysis.

Goodness of fit
Using software PRESENCE v2 (Hines 2006), we performed a goodness of fit test (MacKenzie and Bailey 2004) to evaluate whether our p and ψ-models fit the data, separately for each species. A model is considered to fit the data well if the variance inflation factor ($\hat{c} = \chi^2/DF$) is <3. The fit for the best selected models varied among species (*B. b. spinosus*: $\hat{c} = 5.51$; *B. viridis*: $\hat{c} = 1.41$; *R. temporaria*: $\hat{c} = 1.68$; *R. latastei*: $\hat{c} = 9.34$). We adjusted model selection

criteria and standard errors of the parameters by the variance inflation factors to correct for overdispersion and we applied model averaging to obtain unconditional parameter estimates and standard errors (Burnham and Anderson 2002).

Predicted patterns of occurrence

Because there was considerable model selection uncertainty (see Results), we used model averaging techniques to predict the relationship between explanatory factors and ψ (Burnham and Anderson 2002). We computed predictions (and standard errors) for a range of covariate values for each model and then conducted model averaging on these predictions.

Results

Pond attributes

We observed gradients in all pond characteristics from the riparian forest towards the forest edge, and from the forest edge towards the active tract that contained the habitat types exposed gravel and island edge. For example, pond surface area, pH, and temperature increased, while hydroperiod length, predation risk, and availability of structural elements for egg attachment decreased from the riparian forest towards the active tract (Table 2). Large and shallow ponds were common in the active tract. They exhibited high temperature and pH, and low predation risk, as well as limited structural elements for egg attachment.

Table 2. Descriptive statistics for various factors, separately for different spatial locations in the floodplain.

Location in the floodplain/factor		Mean	SD	Range	
Forest (n =123)					
Ar	Pond surface area	56.143	81.065	0.156	435.691
De	Water depth	0.344	0.291	0.010	1.545
Ebb	Egg density *Bufo bufo*	0.094	0.162	0.000	1.061
Ebv	Egg density *B. viridis*	0.002	0.019	0.000	0.204
Ela	Egg density *Rana latastei*	1.127	3.267	0.000	32.889
Ete	Egg density *R. temporaria*	0.196	0.677	0.000	6.024
Hp	Hydroperiod length	99.600	17.480	5.000	106.000
Ph	pH	7.800	0.311	6.940	8.528
Pr	Predation risk	0.249	0.277	0.000	1.000
St	Structural elements	74.942	20.691	0.000	100.000
T	Temperature	18.974	3.762	12.050	31.600
Forest edge (n =55)					
Ar	Pond surface area	70.752	124.089	0.251	515.619
De	Water depth	0.263	0.260	0.001	1.333
Ebb	Egg density *Bufo bufo*	0.063	0.230	0.000	1.624
Ebv	Egg density *B. viridis*	0.004	0.017	0.000	0.093
Ela	Egg density *Rana latastei*	0.443	1.042	0.000	4.775
Ete	Egg density *R. temporaria*	0.160	0.737	0.000	5.143
Hp	Hydroperiod length	94.58	19.81	35.000	106.000
Ph	pH	7.813	0.287	6.885	8.605
Pr	Predation risk	0.101	0.188	0.000	0.683
St	Structural elements	63.370	20.142	0.000	100.000
T	Temperature	19.129	4.098	12.200	27.354
Island edge (n =97)					
Ar	Pond surface area	72.961	205.278	0.087	1542.129
De	Water depth	0.305	0.277	0.000	1.091
Ebb	Egg density *Bufo bufo*	0.150	0.371	0.000	1.899
Ebv	Egg density *B. viridis*	0.011	0.044	0.000	0.320
Ela	Egg density *Rana latastei*	0.166	0.595	0.000	5.314
Ete	Egg density *R. temporaria*	0.090	0.268	0.000	1.699
Hp	Hydroperiod length	87.900	24.70	8.000	106.000
Ph	pH	7.926	0.234	7.340	8.575
Pr	Predation risk	0.018	0.043	0.000	0.226
St	Structural elements	65.609	18.998	0.000	100.000
T	Temperature	21.476	4.461	13.000	30.100
Exposed gravel (n =78)					
Ar	Pond surface area	169.258	373.616	0.236	2213.652
De	Water depth	0.220	0.182	0.004	1.041
Ebb	Egg density *Bufo bufo*	0.049	0.156	0.000	1.162
Ebv	Egg density *B. viridis*	0.025	0.082	0.000	0.627
Ela	Egg density *Rana latastei*	0.085	0.389	0.000	3.162
Ete	Egg density *R. temporaria*	0.028	0.200	0.000	1.760
Hp	Hydroperiod length	87.22	26.86	3.000	106.000
Ph	pH	8.036	0.241	7.498	8.860
Pr	Predation risk	0.017	0.046	0.000	0.234
St	Structural elements	46.874	26.058	0.000	100.000
T	Temperature	21.643	4.659	13.200	32.400

See Table 1 and Supplementary material Appendix 2 for description of factors.

Rates and probabilities of occurrence

Occurrence rates (% of 353 ponds occupied) that are not corrected for imperfect detection were highest for *B. b. spinosus* (46.7%), followed by *R. latastei* (45.8%), *R. temporaria* (27.7%), and *B. viridis* (13.5%). All four species co-occurred in 1.5% of the ponds. *Bufo b. spinosus* exclusively co-occurred with the two frog species (*R. temporaria*, *R. latastei*) in 17.3% of the ponds. The two frog species exclusively co-occurred in 22% of the ponds, and the two toad species (*B. b. spinosus*, *B. viridis*) exclusively co-occurred in 12.4% of the ponds. Co-occurrence rates were consistently higher than expected by chance (Fig. 2).

Probabilities of occurrence (ψ) that are corrected for imperfect detection were close to the rates of occurrence. *Bufo bufo spinosus* occurred in 46.8% (SE 2.6%) of all ponds. *Bufo viridis* occurred only in ponds in the active tract (13.8% of all ponds, SE 1.85%). *Rana temporaria* occurred in 28.1% (SE 2.3%) and *R. latastei* occurred in 45.8% (SE 2.6%) of the ponds.

Model selection

For all species, there was uncertainty in model selection because several models explained ψ equally well (Table 3, for p-models see Supplementary material Appendix 4). For *B. b. spinosus*, model selection uncertainty was most pronounced. All factors were important. For *B. viridis*, all factors except predation risk and the presence of other species were important. For *R. temporaria*, all factors except temperature and pH were important. For *R. latastei* pond surface area, water depth, the availability of structural elements for egg attachment and the presence of fish were important. Because there was strong overdispersion for *R. latastei*, the results for this species should be interpreted with caution.

Predicted patterns of occurrence

Species used the main habitat types differentially (Fig. 1A). Occurrence of *B. b. spinosus* and *R. latastei* were equally likely across habitat types (Fig. 1A). Both *B. viridis* and *R. temporaria* avoided ponds in the riparian forest.

All species clearly preferred large ponds (Fig. 1B). In addition, both toad species preferred warm ponds (Fig. 1B, E), while temperature was less important for frogs (i.e. confidence intervals included zero). *Bufo viridis* preferred shallow ponds without structural elements for egg attachment (i.e. twigs, branches, aquatic vegetation) while *R. latastei* preferred ponds with opposite characteristics (Fig. 1C, D).

Bufo b. spinosus and *R. latastei* most likely occurred in ponds where the risk of predation was high (Fig. 1F). While *B. viridis* avoided ponds with high predation risk. Breeding site selection of *R. temporaria* did not respond to predation risk (i.e. confidence intervals included zero). The presence of fish (length ≥ 10 cm) positively affected the occurrence of all species, except of *R. temporaria* (Fig. 1G). Species did not avoid ponds that were occupied

Table 3. Model selection results for predicting the probability of occurrence, sorted after differences between Akaike's small sample information criterion (ΔQAICc), corrected for overdispersion with the variance inflation factor ($\hat{c}$). Only models with Akaike weights >0.05 are shown for brevity. For the full model set, see Indermaur (2008).

Model no.	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	Pla	K	ΔQAICc	Qweight	Qdeviance
Bufo b. spinosus: p = (YY+Day+Day^2), $\hat{c}$ = 5.51																				
32							T	T^2	Ph	Ph^2	Fi	Pr		Pbv	Pte	Pla	15	0.00	0.150	536.79
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2							15	1.02	0.090	537.80
9							T		Ph	Ph^2		Pr		Pbv	Pte	Pla	14	1.36	0.076	540.31
31							T	T^2	Ph	Ph^2	Fi						11	1.48	0.072	546.86
5		Ar		De		St	T		Ph	Ph^2							12	1.55	0.069	544.81
41	Ht						T	T^2	Ph	Ph^2	Fi						14	1.63	0.066	540.59
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi						16	2.06	0.053	536.67
B. viridis: p = (Day+Day^2), $\hat{c}$ = 1.41																				
16		Ar		De		St	T		Ph	Ph^2	Fi						12	0.00	0.279	539.78
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi						13	0.01	0.278	537.64
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi						15	1.78	0.115	535.09
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi						14	2.16	0.095	537.64
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi						16	3.04	0.061	534.17
Rana temporaria: p = (YY+Day+Day^2+Ar+Si), $\hat{c}$ = 1.68																				
58											Fi	Pr	Pbb	Pbv		Pla	13	0.00	0.487	1164.57
7		Ar		De		St					Fi	Pr	Pbb	Pbv		Pla	16	2.77	0.122	1160.84
4	Ht										Fi	Pr	Pbb	Pbv		Pla	16	3.06	0.106	1161.12
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv		Pla	18	3.72	0.076	1157.38
R. latastei: p = (YY+Day+Day^2), $\hat{c}$ = 9.34																				
23		Ar		De		St											9	0.00	0.333	331.59
6		Ar		De		St					Fi						10	1.71	0.141	331.20
34		Ar	Ar^2	De	De^2	St											11	2.08	0.118	329.45
27		Ar	Ar^2	De		St					Fi						11	3.42	0.060	330.78
59	Ht	Ar		De		St											12	3.43	0.060	328.66

See Table 1 for description of factors. (.) = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 is the best description of the data given the set of candidate models. Models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (K) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact.
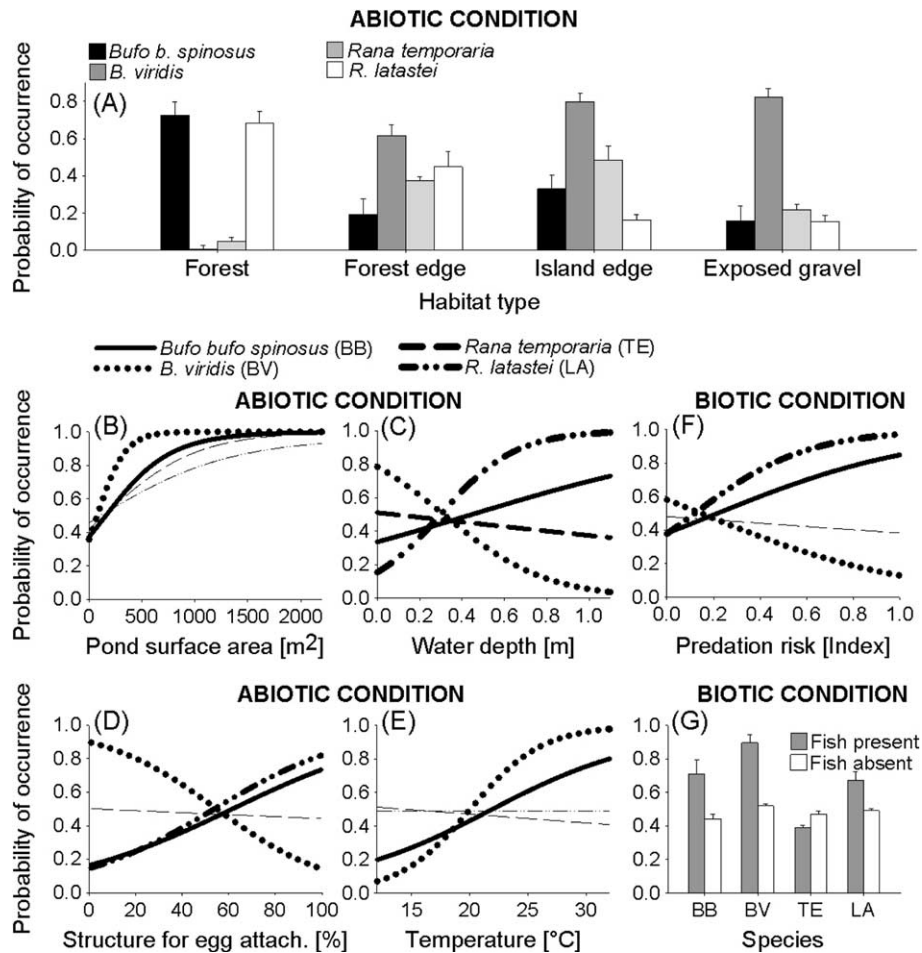
Figure 1. Predicted probability of occurrence for abiotic conditions (A–E) and biotic conditions (F–G). Thick lines denote relationships where the confidence interval for the regression slopes did not include zero. Vertical lines in histograms are upper 95% confidence interval. Predictions for panel A refer to mean values of the continuous covariables and when fish were absent; predictions for panels B–E refer to mean values of the non-focus continuous covariables, to habitat type forest edge and to ponds without fish; predictions for panel G refer to mean values of the continuous covariables and habitat type forest edge.

by other species. In contrast, the presence of other species had positive effects on occurrence. In summary, species pairs differed in their response to at least one factor (Table 4, Supplementary material Appendix 6). One such factor was the availability of structural elements for egg attachment (Fig. 1D).

Table 4. Comparison of species pairs in relation to factors for which species differed in their response, i.e. while breeding site selection of one species was positively related to a specific factor, breeding site selection of the other species was negatively related to the same factor.

	Bufo b. spinosus	B. viridis	Rana latastei	R. temporaria
Bufo b. spinosus	.	St, De, Pr*	T*, De*	T*, Fi*, Pr*
B. viridis		.	St, De, T*, Pr*, seasonal	Fi*, seasonal
Rana latastei			.	De*, Fi*, Pr*
R. temporaria				.

See Table 1 for description of factors. *for one of the two species, the factor included zero in 95% confidence intervals.

Discussion

Our results demonstrate that the joint effects of the abiotic and biotic environment govern local breeding site selection of anurans in a dynamic floodplain. Species differed in the use of the main habitat types (Fig. 1A). When ponds in the same habitat type were used by multiple species, they were used differentially in relation to abiotic and biotic factors (Fig. 1). Species preferred ponds that were occupied by other anuran species and fish (Fig. 1G). Hence, competitor avoidance currently appears to play a minor role in breeding site selection and local co-existence. Rather differential selection of shared habitat types in relation to abiotic conditions and predation risk permit co-existence in the larval anuran community at the pond-level.

Predicted patterns of occurrence

We propose two explanations for the high rates of species co-occurrence, and the lack of support for competition observed: 1) seasonal segregation, and 2) niche differentiation along environmental gradients. Our results

strongly support niche differentiation, but not seasonal segregation.

1) The rate of co-occurrence of *B. b. spinosus* with frogs (*R. temporaria*, *R. latastei*) was 17.3% and with *B. viridis* 12.4%, and all species co-occurred in 1.5% of ponds, which is higher than expected by chance (Fig. 2). The parameter estimates indicated that frogs avoid *B. viridis*. However, *B. viridis* was absent from the ponds when frogs selected breeding sites (Indermaur unpubl.). In fact, species with overlapping breeding periods (Supplementary material Appendix 6: *B. b. spinosus* with frogs, *B. b. spinosus* with *B. viridis*), preferably colonized ponds that were occupied by other species. Hence, the low proportion of shared ponds of all four species was due to the late breeding period of *B. viridis* rather than competition avoidance. Seasonal segregation is therefore unlikely to facilitate co-existence in anurans (Alford and Wilbur 1985, Lawler and Morin 1993, Vignoli et al. 2007).

2) Species differed in the use of the main habitat types (Fig. 1A) and they differentially used ponds in the same habitat types based on biotic and abiotic conditions. Nevertheless, species co-occurred more often than expected by chance (Fig. 2). This happened because the same pond characteristics were favourable for more than one species (e.g. all species preferred larger ponds). Hence, some ponds tend to be "good" environments for all species, including not only anurans but also fish. We therefore predicted local species diversity of anurans to identify the habitat characteristics that may constitute diverse freshwater communities. Local anuran diversity was highest in large, warm, deep and structurally complex ponds (Supplementary material Appendix 7), in line with classical expectations (MacArthur and MacArthur 1961, Pianka 1967).

When examined in detail, the species selected breeding sites differently in relation to abiotic and biotic factors (Table 4, Fig. 1). Our results therefore support the view that co-existence is facilitated through some degree of niche-differentiation along environmental gradients, consistent with similar findings by earlier studies (Werner and McPeek 1994, Van Buskirk 2003, Richter-Boix et al. 2007). However, our results join other results (Van Buskirk 2007) that do not support the role of competition in breeding site selection, thereby contrasting with classical expectations (Gause 1934, Hardin 1960) and empirical
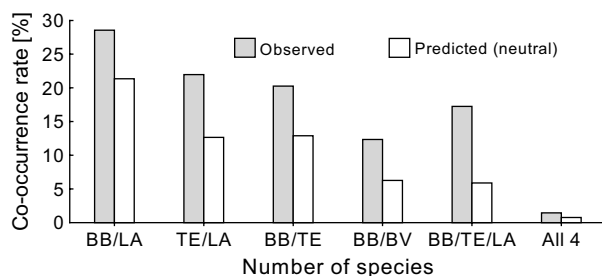

Figure 2. Observed and predicted rates of co-occurrence. Co-occurrence rates are given for two, three, and four species ("All 4"). Predicted rates of co-occurrence (multiple species), independently of the presence of other species ("neutral"), are the products of rates of occurrence of single species (see Results section). BB = *Bufo b. spinosus*, BV = *B. viridis*, TE = *Rana temporaria*, LA = *R. latastei*.

studies (Hairston 1980, Wilbur and Alford 1985, Resetarits and Wilbur 1989, Laurila 2000, Bardsley and Beebee 2001). In a previous study where anuran diversity in the dynamic floodplain was investigated, the authors ascribed the high species diversity observed to the typically high structural organization of unpredictable environments (Tockner et al. 2006). Disturbances that maintain high structural diversity and environmental gradients are therefore most probably fundamental to the high local species diversity observed (Connell 1978).

In the following, we discuss differential habitat preferences in more detail to shed light on differences in the species' tolerance to limiting factors. All species selected breeding sites in relation to water depth, which is a surrogate for hydroperiod length (Fig. 1C). Species, however, preferred either deep or shallow ponds, which re-emphasizes the importance of gradients in hydroperiod for the distribution and composition of freshwater communities (Werner and McPeek 1994, Wellborn et al. 1996, Van Buskirk 2003).

Toads preferably used warm and large ponds, while frogs selected ponds independent of temperature and the size of ponds (Fig. 1B, E). The selection of large and warm ponds by toads implies improved larval performance. Indeed, in an earlier study we showed that larvae of *B. b. spinosus* grew quickly to a large size at metamorphosis in warm and large ponds of the active tract (Indermaur 2008). In cold forest ponds, *B. b. spinosus* slowly grew to small metamorphic size. Moreover, production of metamorphs was about one to two orders of magnitude smaller in the riparian forest than in the active tract (Indermaur 2008). These results imply that larger ponds are more productive than small ponds, and that higher temperatures are needed to process food, and hence promote growth of toad larvae. Furthermore, the habitat type-specific growth rates observed (Indermaur 2008) clearly show that habitat selection is a fitness relevant process with potential impacts on population dynamics (Werner et al. 1983).

Water depth and predation risk were the two main factors that separated all four species in breeding site selection and probably facilitate their co-existence (Table 4; Fig. 1; Supplementary material Appendix 6). For example, the toad *B. viridis* and the frog *R. temporaria* most likely occurred in low-predation risk ponds, which because of frequent drying and flooding, are typical for the active tract (Table 2; Fig. 1A). That *B. b. spinosus* and *R. latastei* most likely occurred in high predation risk ponds of the riparian forest, however, is less intuitive. Moreover, adult amphibians are known to perceive the presence of predators that consume their larvae (Resetarits and Wilbur 1989, Rieger et al. 2004). It seems that a positive correlation between predator and prey density can occur (Van Buskirk and Schmidt 2000) when the usually higher productivity in high-predation risk environments outweighed negative effects of predation (Reznick et al. 2001, Thurnheer and Reyer 2001, Peacor 2002).

We conclude that differential response to abiotic conditions and predation risk within shared habitat types permit temporal co-existence in the larval anuran community studied at the pond-level (Alford and Wilbur 1985, Lawler and Morin 1993, Vignoli et al. 2007). This result is similar to our study on terrestrial habitat selection of toads

(Indermaur et al. 2009), suggesting that differential habitat selection within shared habitat types is evident in all life history stages of species with complex life cycles. Our results do not support the pervasive role of competition in governing breeding site selection and hence co-existence. The typically large variation in environmental conditions, maintained by disturbances such as floods, most probably outweighed competitive effects (Gallet et al. 2007), thereby facilitating the high local anuran diversity observed. Other studies predicted regional species diversity accurately assuming neutral processes (Hubbell 2001, Muneepeerakul et al. 2008). Based on our results we can clearly reject the neutral model, as most species combinations were found locally co-existing in higher frequency than expected by chance (Fig. 2).

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