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Recovery of anuran community diversity following habitat replacement

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Summary

1. Recently habitat degradation, road construction and traffic have all increased with human populations, to the detriment of aquatic habitats and species. While numerous restoration programmes have been carried out, there is an urgent need to follow their success to better understand and compensate for the decline of amphibian populations. To this end, we followed the colonization success of an anuran community across multiple replacement ponds created to mitigate large-scale habitat disturbance.

2. Following construction of a highway in western France, a restoration project was initiated in 1999 and the success of restoration efforts was monitored. The amphibian communities of eight ponds were surveyed before they were destroyed. Replacement ponds were created according to precise edaphic criteria, consistent with the old pond characteristics and taking into account the amphibian species present in each. The presence of amphibian species was recorded every year during the breeding period for 4 years following pond creation.

3. Species richness initially declined following construction of the replacement ponds but generally returned to pre-construction levels. Species diversity followed the same pattern but took longer to reach the level of diversity recorded before construction. Pond surface area, depth and sun exposure were the most significant habitat characteristics explaining both amphibian species richness and diversity. Similarly, an increase in the number of vegetation strata was positively related to anuran species richness, indicating the need to maintain a heterogeneous landscape containing relatively large open wetland areas.

4. *Synthesis and applications.* We highlight the species-specific dynamics of the colonization process, including an increase in the number of replacement ponds inhabited over time by some species and, in some cases, an increase in population size. Our work suggests that successful replacement ponds can be designed around simple habitat features, providing clear benefits for a range of amphibian species, which will have positive cascading effects on local biodiversity. However, consideration must also be given to the terrestrial buffer zone when management strategies are being planned. Finally, our study offers insight into the successful establishment of anuran communities over a relatively short time in restored or replacement aquatic environments.

Key-words: anurans, colonization, community persistence, mitigation plan, pond restoration, Simpson's diversity index, species richness

Introduction

The decline of amphibian populations throughout the world is well established (Houlahan *et al.* 2000). Although the debate about the causes of these declines continues (Alford & Richards 1999), habitat destruction (Blaustein & Kiesecker 2002), pollution (Hecnar & M'Closkey 1996a), road mortality (Hels

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& Buchwald 2001) and interactions between climatic variability, UV-B radiation and disease (Kiesecker, Blaustein & Belden 2001) have been recognized as the primary threats. In recent decades, habitat degradation or alteration, road construction and traffic have all increased concomitant with human population growth (Beebee 1997; Forman & Alexander 1998). Efforts have been made to mitigate these threats but the critical factors for successful habitat restoration for amphibians are still unknown (Cushman 2006; Loman & Lardner 2006). For instance, conservation measures commonly used to counteract habitat destruction include translocation (Seigel & Dodd 2002; Germano & Bishop 2009) and creation of new or restoration of old wetlands (Semlitsch 2000). However, evaluation of the efficacy of these mitigation measures is still lacking (but see Petranka, Kennedy & Murray 2003a; Petranka, Kennedy & Murray 2003b; Vasconcelos & Calhoun 2006). Furthermore, a multispecies approach to evaluating and monitoring conservation efforts is needed (Maes & Bonte 2006).

One goal when restoring wetlands is to provide suitable habitat for native wetland species, including pond-breeding amphibians. Although the most important elements for successful recovery of amphibians are known, with key factors ranging from the maintenance of aquatic habitat quality to the number of translocated tadpoles required to achieve a target population size (Kentula *et al.* 1993; Semlitsch 2002), a recent review by Pullin *et al.* (2004) showed that the majority of conservation actions remain experience-based and rely heavily on traditional land management practices and conjectures. In fact, many management actions remain unevaluated and although some evidence exists supporting their implementation, little information is readily accessible in a suitable form for conservation managers. Post-construction monitoring of wetlands is rare and few studies present data on mitigation success (Semlitsch 2002; Petranka *et al.* 2003a,b; Pullin *et al.* 2004; Vasconcelos & Calhoun 2006). Lehtinen & Galatowitsch (2001) showed that recently restored wetlands were valuable habitat for only a subset of the amphibians present on reference sites. However, in their study, the oldest wetland was surveyed 20 months after its creation, which is less than the time required by most aquatic-breeding amphibians to reach reproductive maturity. Therefore, solid conclusions concerning the establishment of viable populations were difficult to make (Reed *et al.* 2003). In contrast, Pechmann *et al.* (2001) monitored breeding amphibian population sizes and juvenile recruitment at newly created ponds over 8·5 years, comparing the populations with others at the original wetland and at an undisturbed reference wetland. Replacement ponds compensated for wetland loss, but differed in community structure. However, in that study, a large bay was replaced with some very small ponds which were different in many important respects, hence meaningful comparisons are quite difficult to make. While these studies are valuable, there is a need for comparable studies including continuous observation of amphibian population loss together with survey data from locally restored wetlands. The results from such studies may help to assess the potential effects of wetland restoration on local and global amphibian population declines.

Following the construction of a highway in western France in1999 and the subsequent destruction of ponds, replacement ponds were built and surveyed over the following 4 years, providing the opportunity to evaluate the effectiveness of a restoration programme. Our research focused on the phenology of the colonization of new ponds by amphibians and we predicted that monitoring for 2–3 years would be sufficient to identify species that will use the ponds for the first decade or so after pond creation (Petranka *et al.* 2003a). Since the landscape surrounding wetlands is important for key processes, such as dispersal and population dynamics (Ficetola, Padoa-Schioppa & De Bernardi 2009), we also hypothesized that habitat features other than pond size will influence species richness and diversity. In particular, we predicted a positive relationship between sun exposure (in regards to tadpole development) and the number of vegetation strata (in regards to food resources) with species richness and/or diversity. By contrast, pond depth (which decreases average water temperature) and shoreline cover (which might affect pond access) are both predicted to have a negative impact on species richness and diversity.

Materials and methods

GENERAL STUDY SITE INFORMATION

The study area lies within the Maine & Loire region of western France along a highway transect delimited by the cities of Angers and Cholet. The restoration project included the construction of eight ponds to replace those that were destroyed along the highway. The ponds were considered independent since they were separated by an average distance of 17 km (range 5·5–34·5 km) and it is unlikely that individuals moved between any of these ponds during the study period. Like most of the amphibian breeding habitats in this area, the original ponds were man-made, often dug out to provide drinking places for livestock. Although no wetland can be replicated identically (Kustler & Kentula 1990), the eight new ponds were built during the autumn at the same time as the old ones were filled with soil. The new ponds were built in the vicinity of the previous sites (range 80–120 m) and all physical characteristics (surface area, depth, bank slopes) were designed to be as similar as possible to the old ponds to allow reasonable comparisons. New ponds were lined with 40–50 cm of clay so that they would collect and hold rainwater. Although water level fluctuated over the first 2 years, all ponds were reasonably full by mid-January of the first year when the first species began breeding and the ponds have remained permanent ever since. We used a 'self-designed' approach (Mitsch & Wilson 1996) in assuming that the newly created ponds had a high probability of being colonized by local plant species (Lichko & Calhoun 2003). New ponds were not stocked since amphibian activity was limited during the autumn and stocking would probably have resulted in a bias among ponds. Replacement ponds filled naturally with rainwater and experienced unrestricted colonization and succession.

SPECIES INVENTORIES

From 1999 to 2003, a species inventory was assembled by conducting repeated visits to focal ponds from mid-January to mid-July. Each pond was visited up to three times a week with daily visits during the breeding season of each species. Standardized frog survey techniques were employed at each site. Species occurrence was determined by

audio strip transect sampling and visual transect sampling at night when most amphibian activity occurs (Jaeger 1994; Zimmerman 1994). Estimated population size for each species was based on the maximum number of calling males (less than or equal to male population size) and clutch counts (less than or equal to breeding female population size) in and around each pond. The pond margins and, whenever possible, most of the pond area were visited and amphibian adults, eggs or larvae were censused by visual searches and dip-netting. Identification was carried out in the field; all adults, adult calls and clutches are easily distinguished (except for the species of the hybridogenetic *Rana esculenta* complex: *Rana lessonae/ridibunda/kl. esculenta* = *Rana LRE* hereafter; Semlitsch *et al.* 1996a,b). To standardize the survey methodology, we adjusted the time spent on each site according to the pond size and habitat complexity so that every 10 m of shoreline was surveyed during an average of 3·4 (±0·4) person-hours during the season. Based on our experience of repeated measure surveys of many similar habitats in the same area over the past 20 years, this approach maximized the probability of detecting all species present in the pond on any given visit (Lesbarrères & Lodé 2002).

HABITAT VARIABLES

We conducted plant surveys in 2003 to assess the influence of vegetation on species occurrence. Based on recent studies of habitat features and amphibian diversity (Crochet *et al.* 2004; Ficetola & de Bernardi 2004), we restricted our analyses to the variables known to influence our study species. The number of vegetation strata (STRATA) was used to estimate the diversity of site vegetation: tree stratum (woody plants > 10 cm d.b.h. or > 5 m height), shrub and bush stratum (woody plants < 10 cm d.b.h. or < 5 m height), floating vegetation stratum (herbaceous vegetation with submerged stems and floating leaves), submerged vegetation stratum (herbaceous vegetation that is completely or mostly submerged), helophyte stratum (herbaceous plants rooted in flooded habitat but with most of the stem/leaves emergent out of the water), low herbaceous stratum (< 50 cm height), medium herbaceous stratum (50–100 cm height) and high herbaceous stratum (> 100 cm height). We recorded the presence/absence of each species in the different strata. The proportion of vegetation cover was estimated by eye to describe permanent pond and shoreline cover (PONDcov and SHOREcov, respectively). Values for this variable ranged from 0% (no vegetation cover) to 100% (full vegetation cover). We estimated sun exposure (SUN) as the proportion of the pond that was directly exposed to sunlight (using 5% steps) between 11:00 and 1:00 hours (UTM) in February and May during sunny days (between 20 to 24 days for each pond). We averaged sun exposure on all days sampled to give mean sun exposure over the breeding season. Finally, surface area (AREA) and maximum depth (DEPTH) of each pond were estimated using a decametre (±0·1 m).

Fish and predatory invertebrate presence have also been shown to be important factors influencing amphibian diversity (Semlitsch & Gibbons 1988; Gibbons *et al.* 2006) but we were unable to collect relevant data in any of the replacement ponds during the study period.

STATISTICAL ANALYSIS

We estimated restoration success by comparing species diversity before and after sites were restored. We estimated population size, species richness (S) and Simpson's reciprocal diversity index $D = 1/\lambda_j$ with $\lambda_j = \Sigma p_i^2$, where p_i is the frequency of the species i in site j (Simpson 1949). For each pond, D ranges between 1 and S. Higher values indicate greater sample diversity. We compared species diversity in the newly constructed ponds and the original ponds from S and D estimates between 1999 and 2003 using t-tests for dependent samples.

We recorded the presence or absence of each species in each pond in each year to determine the proportion of replacement ponds that were inhabited by each species over time and the proportion of the anuran species richness in each pond. We applied logistic regression to the presence/absence values, using time after the destruction of the original ponds as the independent variable. Finally, to investigate the influence of time on population size, we looked at the interaction between species and year in a repeated-measures ANOVA with year as repeated factor.

The replacement ponds were allowed to colonize with plants naturally over the survey period. Therefore, to test the influence of habitat characteristics on biodiversity indices, data from 2003 were analyzed with multiple linear regression, with the most appropriate model being selected using Akaike Information Criteria methods (Burnham & Anderson 2002; see Supporting Information for full model comparison). We first tested for multi-collinearity using the correlation matrix between variables (AREA; DEPTH, SUN, STRATA, PONDcov and SHOREcov): if $r > 0{\cdot}7$, then the regression may be biased (Berry & Fieldman 1985). While the correlation between DEPTH and SUN was 0·624 and between SUN and STRATA was −0·507, in all pairwise correlations $r < 0{\cdot}7$ ($P > 0{\cdot}098$ in all cases) and hence multi-collinearity was not considered a serious problem in our data set. Multiple regression models were developed by including all combinations of independent habitat variables. All statistical analyses were performed using the SPSS Statistical Package v.11·5 (SPSS Inc., Chicago, IL, USA) and Matlab v7·0·4·352 (The Math Works, Natick, MA, USA).

Results

Six frog species were recorded in this area including the earliest breeders *Rana dalmatina* and *Bufo bufo* and the latest breeders *Rana* LRE and *Hyla arborea* as well as *Pelodytes punctatus* and *Alytes obstetricans*. For the eight ponds studied, the mean surface area was 628·66 m^2 (SD = 887·72), mean depth was 1·68 m (SD = 0·63), mean sun exposure was 74·38% (SD = 33·11), mean pond cover was 33·13% (SE = 31·62), mean shoreline cover was 91·88% (SE = 11) and the mean number of strata was 4·63 (SE = 1·51).

RESTORATION SUCCESS

Five out of the six species observed in the old ponds in 1999 were present in the new ponds by 2003 and successful reproduction (clutches, tadpoles, froglets) was observed for four of the six anuran species recorded (*B. bufo, R. dalmatina, R. LRE, H. arborea*) in the following years. No evidence of successful reproduction has been recorded for *P. punctatus* and *A. obstericans*. Species richness did not differ between the original (destroyed) and the new (replacement) ponds at the end of the survey period (3·25 and 3·63 species per pond in 1999 and 2003, respectively; $t = -1{\cdot}26$, d.f. = 7, $P = 0{\cdot}25$, Fig. 1a) although this result could be related to low statistical power. Likewise, diversity returned to levels observed in the old ponds as we did not observe a significant difference between diversity scores in 1999 and 2003 ($t = 0{\cdot}36$, d.f. = 7, $P = 0{\cdot}73$, Fig. 1b).

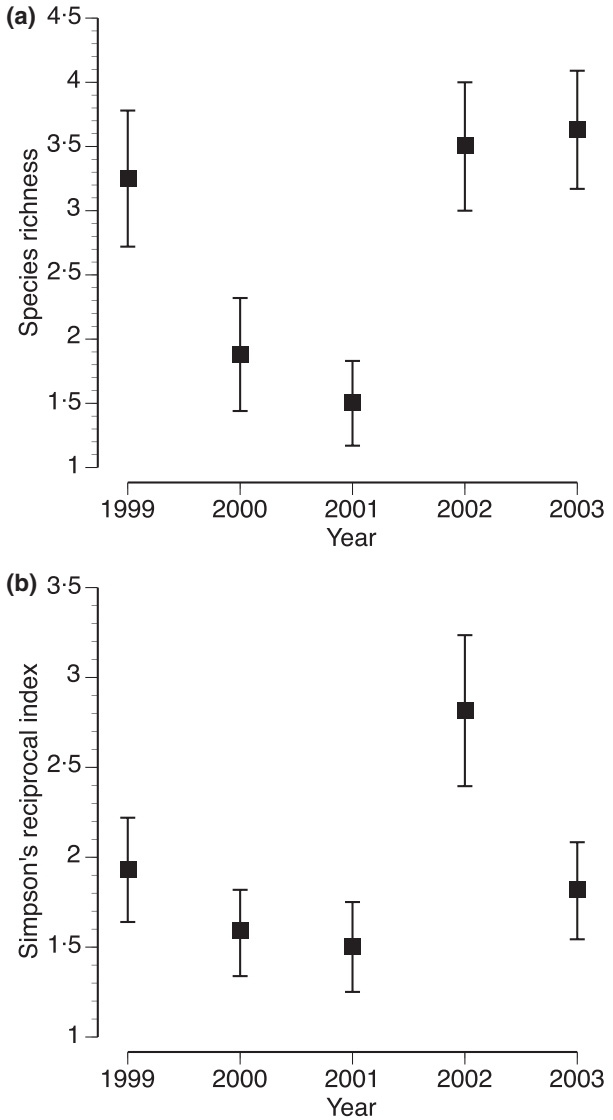

Fig. 1. (a) Mean species richness (±SE) and (b) mean Simpson reciprocal diversity index (±SE) among the eight ponds for each year of the study. The values for 1999 are from censuses of the original ponds, values from 2000 onwards are censuses of the replacement ponds.

The recovery of the anuran communities over time differed both at the level of individual species and ponds (Figs 2 and 3). The results of the logistic regression confirmed that most species inhabited more replacement ponds over time (Fig. 2, Table 1 – here, the sign of the regression coefficient indicates the direction of change in the probability that each species would be found in all replacement ponds over time). The proportion of ponds occupied by each species varied but there was a significant increase in two species (*R. dalmatina* and *B. bufo*; Fig. 2a and e). By contrast, there was a decline in the proportion of ponds occupied by *A. obstetricans* because in 2001, it disappeared from the area in which it had been observed prior to pond destruction (Fig. 2f). There was an increasing trend in the proportion of the anuran community that was present in each pond over the study period, but only two of these were significant (Les Challonges and La Frétellière, Fig. 3, Table 2).

Temporal fluctuations were observed in the population size with a significant interaction between species and year (Repeated-measures ANOVA, $F_{20,168} = 2{\cdot}4$, $P = 0{\cdot}001$) and an increase in population size beginning in 2002 for *R. dalmatina* and *B. bufo* (Fig. 4).

FACTORS INFLUENCING SPECIES RICHNESS AND DIVERSITY

A model including surface area, pond depth, mean sun exposure and number of strata explained 96·3% of the variation in species richness in 2003 ($F_{4,3} = 19{\cdot}67$, $P = 0{\cdot}017$; Table 3 and Table S1 in Supporting Information). The best model of species diversity included surface area, pond depth, mean sun exposure and SHOREcov ($F_{4,3} = 17{\cdot}42$, $P = 0{\cdot}02$, $r^2 = 0{\cdot}96$; Table 3, Table S2). We did not find any significant effect of pond vegetation cover on species richness or diversity.

Discussion

Denton *et al.* (1997) pointed out that measures of restoration success for amphibians should be estimated as: (i) initial success, the emergence of metamorphs from ponds; (ii) intermediate success, return of adults to breed for the first time; (iii) complete success, continuation of breeding for 5 years; and (iv) failure, adults fail to return after 5–10 years. Our observations suggest that the restoration ponds met the first two criteria and we are optimistic about the medium- to long-term local survival of the species of interest.

RESTORATION SUCCESS

In our study, the newly created ponds appear to have successfully mitigated the loss of the original ponds, with the exception of the midwife toad A. *obstetricans*, which was rare in the original ponds. The newly created ponds provided suitable habitat for breeding and larval development for many of the species. Ultimately, species richness and diversity in the new ponds in 2003 was similar to that recorded in 1999 in the old ponds. However, species richness varied substantially among years. Extensive temporal fluctuations have also been reported in other amphibian populations and communities, both on undisturbed (Berven 1990; Semlitsch *et al.* 1996a,b; Meyer, Schmidt & Grossenbacher 1998) and newly created wetlands (Arntzen & Teunis 1993; Pechmann *et al.* 2001) suggesting that a minimum of 5–6 years of census data are necessary for meaningful evaluation of restoration projects (Arntzen & Teunis 1993). However, taking into consideration the time lags associated with the juvenile stage, it is likely that viable populations of most species have now established because (i) successful reproduction has been observed for four out of the six anuran species recorded during the study; and (ii) populations still persist to date with year-on-year recaptures (D. Lesbarrères & A. Pagano, unpublished data). As predicted, species richness decreased significantly from 1999 to 2001 before an increase in 2002 (Fig. 1) indicating an approximate 3-year recovery time

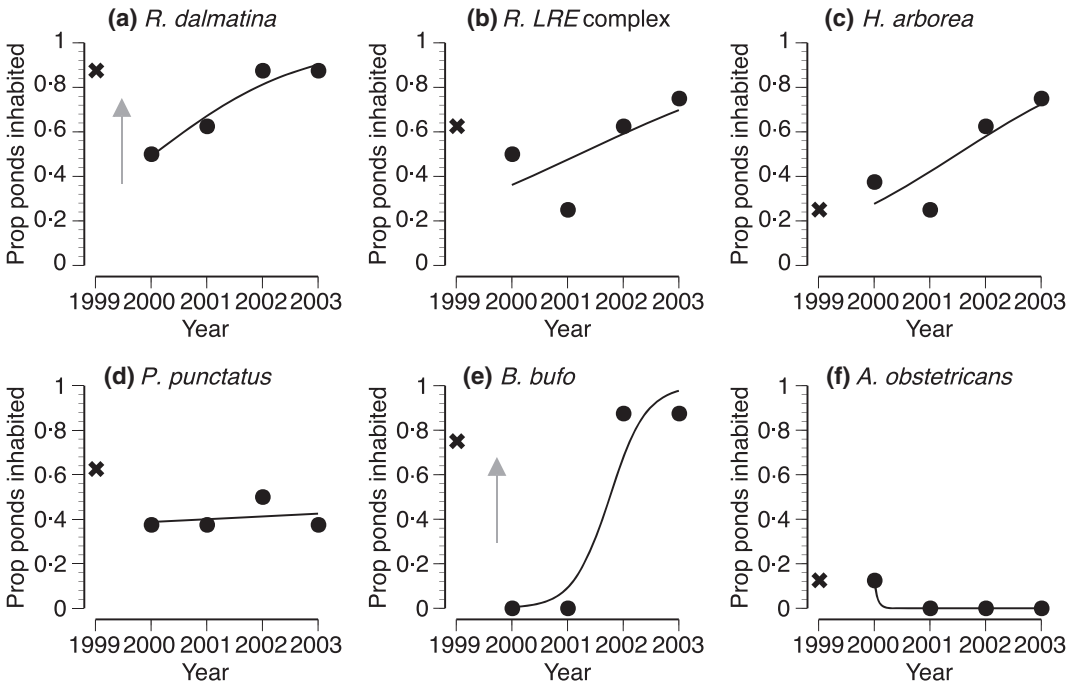

Fig. 2. Changes in the proportion of all ponds inhabited by each anuran species over time. The values for 1999 are from censuses of the original ponds (✖), values from 2000 onwards are censuses of the replacement ponds (●). Panels also show logistic regression lines for the change in the presence/absence of each species in all replacement ponds. (a) *Rana dalmatina*, (b) *Rana LRE*, (c) *Hyla arborea*, (d) *Pelodytes punctatus*, (e) *Bufo bufo*, (f) *Alytes obstetricans*. Species that showed a significant increase (↑) or decrease (↓) in the proportion of ponds inhabited over the study period are marked in the panels with grey arrows.

Table 1. Logistic regression statistics for the probability that all replacement ponds are inhabited by each species

Pond site	Regression coefficient (±SE)	Intercept (±SE)	Deviance	G^2 statistics	*P*-value
Rana dalmatina	0·751 (0·409)	−0·790 (0·960)	0·366	3·292	0·048
Rana LRE	0·469 (0·335)	−1·038 (0·902)	2·496	2·070	0·150
Hyla arborea	0·641 (0·350)	−1·603 (0·951)	1·478	3·719	0·054
Pelodytes punctatus	0·052 (0·322)	−0·509 (0·886)	0·358	0·026	0·87
Bufo bufo	3·020 (1·064)	−8·327 (3·026)	5·191	26·613	< 0·001
Alytes obstetricans	−61·166 (6×10^6)	59·220 (6×10^6)	0	2·872	0·090

Year after destruction of the original ponds was used as the independent variable. In all cases d.f. = 1.

among ponds. In fact, heavy road work continued in the vicinity of the ponds during 2000 and part of 2001 that could have prevented earlier colonization. Earlier colonization may have occurred if the replacement ponds and surroundings were created before the original ponds were destroyed (Lehtinen & Galatowitsch 2001).

POND COLONIZATION

Temporal variation in pond colonization was observed among species indicating species-specific colonization ability and habitat requirements. The disappearance of *A. obstetricans* from the only area where it was present suggests a failure to provide suitable habitat for this species. We chose not to stock the ponds but if wetland creation is being undertaken primarily for the benefit of rare or endangered species, our results indicate that there is no guarantee they would become established in the new habitat without additional help (Kustler & Kentula 1990) and that transfer of individuals to new sites could be advantageous (Gilioli *et al.* 2008). The increase in the number of ponds occupied by tree frogs *H. arborea* indicates a strong colonization ability (Stumpel & Hanekamp 1986; Fog 1993): it can cross barriers that are insurmountable for more terrestrial amphibians and the species survives well in temporary wetlands (Pavignano, Giacoma & Castellano 1990). Furthermore, Ficetola & de Bernardi (2004) showed that tree frogs prefer sunny wetlands which are likely to be a feature of artificially created ponds before plants become well established thereby favouring early colonization by this species. Similarly, our records of widespread colonization by *B. bufo* are consistent with a previous study showing high numbers of this species in new ponds (Baker & Halliday 1999). Although the new ponds were at least 850 m from other wetland areas (e.g. Le Doua), colonization from more distant ponds cannot be excluded

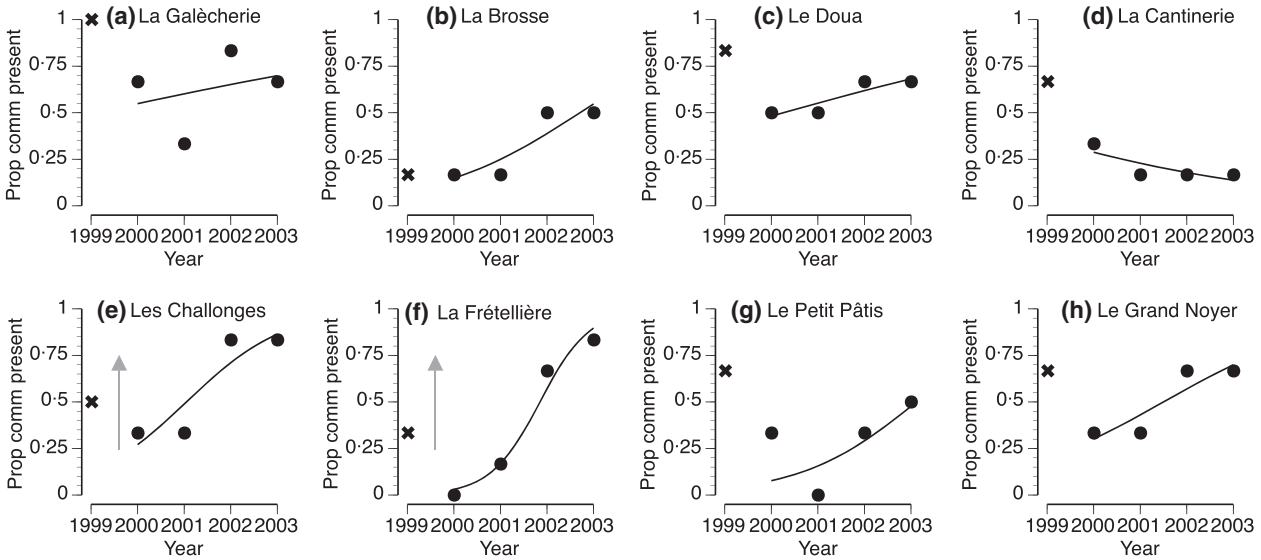

Fig. 3. Changes in the proportion of the sampled anuran communities that are present in each pond over time. The values for 1999 are from censuses of the original ponds (✖), values from 2000 onwards are censuses of the replacement ponds (●). Panels also show logistic regression lines for the change in the presence/absence of the sampled community that was found in each pond. (a) La Galècherie, (b) La Brosse, (c) Le Doua, (d) La Cantinerie, (e) Les Challonges, (f) La Frétellière, (g) Le Petit Pâtis, (h) Le Grand Noyer. Ponds that showed a significant increase (↑) or decrease (↓) in the proportion of the anuran community inhabiting them over the study period are marked in the panels with grey arrows.

Table 2. Logistic regression statistics for the probability that all sampled frogs in the community are found in each replacement pond

Pond site	Regression coefficient (±SE)	Intercept (±SE)	Deviance	G^2 statistics	*P*-value
La Galècherie	0·215 (0·382)	−0·020 (1·021)	3·113	0·321	0·571
La Brosse	0·645 (0·432)	−2·390 (1·275)	0·618	2·486	0·115
Le Doua	0·278 (0·378)	−0·350 (1·013)	0·137	0·552	0·457
La Cantinerie	−0·309 (0·463)	−0·597 (1·170)	0·246	0·459	0·498
Les Challonges	0·945 (0·457)	−1·936 (1·157)	1·237	5·275	0·022
La Frétellière	1·875 (0·712)	−5·341 (2·068)	0·824	13·326	< 0·001
Le Petit Pâtis	0·797 (0·501)	−3·283 (1·568)	2·624	3·006	0·083
Le Grand Noyer	0·562 (0·395)	−1·404 (1·076)	0·530	2·188	0·139

Year after destruction of the original ponds was used as the independent variable. In all cases, d.f. = 1.

(Marsh & Trenham 2001; Gibbons 2003). Likewise, while the new ponds were unsuitable for re-colonization immediately after construction, other ponds in the area could have acted as 'buffers' to support breeding activity. The aim of our study, however, was to assess the restoration success of the new ponds in providing breeding habitat for amphibians and not to study differences in population demographics between new and old ponds. Therefore, it is possible that the populations observed in the new ponds originated both from the old ponds and from other nearby ponds.

ENVIRONMENTAL CORRELATES OF SPECIES DIVERSITY

There was temporal variation in the amphibian diversity in the newly created ponds and surface area was found to be one of the main factors influencing species richness and diversity (Table 3). Although this result sounds intuitive, in our study it may have been driven by two cases where the size of the old pond could not be reproduced at the new site. For example, at La Brosse species diversity increased steadily from 1999 to 2003 and the surface area of the old pond was 10 m^2 whereas the new pond presented a permanent surface area of 98 m^2, potentially allowing more species and/or larger populations to coexist (Lehtinen & Galatowitsch 2001). In contrast, species diversity decreased steadily over time at La Cantinerie. Although the surface area increased from 1250 to 2760m^2, the number of strata decreased from eight to four and absolutely no vegetation covered the pond, limiting the attractiveness to some amphibians whose clutches are attached to submerged and emergent sticks and vegetation. In our study, pond size and habitat heterogeneity (number of vegetation strata) were two important factors driving species richness and diversity in the ponds 4 years after creation. While smaller restored wetlands are probably colonized more slowly than larger ones, our data are consistent with studies showing a relationship between amphibian species richness and wetland size (Hecnar & M'Closkey 1996b; Snodgrass *et al.* 2000) as well as the importance of landscape elements around the ponds (Ficetola *et al.* 2009). Furthermore, although aquatic predators like fish and

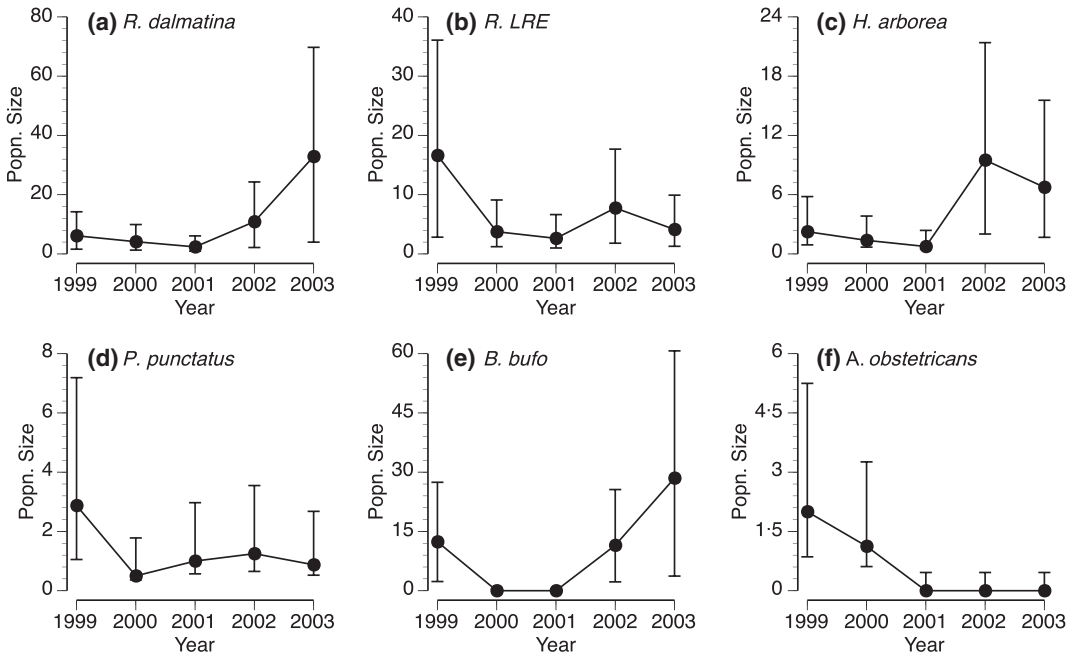

Fig. 4. Temporal variation of the species estimated mean population size taken across all eight ponds, with 95% confidence intervals from a Poisson distribution for each year of the study. Estimated population size for each species was based on the maximum number of calling males (less than or equal to male population size) and clutch counts (less than or equal to breeding female population size) in and around each pond. The values for 1999 are from censuses of the original ponds, values from 2000 onwards are censuses of the replacement ponds.

Table 3. Best model of linear multiple regression for species richness (for full list of model comparisons, see Table S1) and Simpson's reciprocal diversity index (full list of model comparisons, see Table S2) across eight ponds sampled in 2003

	Species richness					Species diversity			
	Parameter coefficient	R^2-value	*F*-value	*P*-value		Parameter coefficient	R^2-value	*F*-value	*P*-value
Full model		0·963	19·668	0·017	Full model		0·959	17·424	0·020
Partial statistics					*Partial statistics*				
Intercept	1·169	0·374	1·796	0·273	Intercept	3·514	0·842	16·039	0·03
Surface area	0·001	0·944	50·501	0·006	Surface area	0·002	0·874	20·837	0·020
Depth	−2·516	0·924	36·520	0·009	Depth	−0·892	0·860	18·471	0·023
Sun	0·053	0·915	32·464	0·011	Sun	0·021	0·902	27·675	0·013
STRATA	0·756	0·885	23·060	0·017	SHOREcov	−0·016	0·490	2·881	0·188

Best model: species richness = 1·1691 + 0·0012 × Area − 2·5161 × Depth + 0·053 × Sun + 0·7562 × STRATA.
Best model: species diversity = 3·5139 + 0·002 × Area − 0·8919 × Depth + 0·0213 × Sun − 0·0161 × SHOREcov.

aquatic invertebrate were not recorded is this study, it is important to monitor their presence in old vs. new ponds as they could affect the specific colonization probabilities (Semlitsch & Gibbons 1988). More generally, distinguishing the driving forces behind community fluctuations requires detailed knowledge of species' demography, interactions with other community members and responses to environmental variation (Ranta *et al.* 2008; Ruokolainen *et al.* 2009).

MANAGEMENT IMPLICATIONS

Our results highlight the fact that although the communities at most of the replacement ponds seem to have recovered well over our relatively short study period, caution is still required. In particular, reductions in species diversity in the replacement ponds at La Cantinerie and La Galècherie compared with the destroyed ponds suggest that careful monitoring is required, if not further modification of these sites would be needed to make them more suitable for anurans. Similarly, *A. obstetricans* has been lost from the only site where it was previously found, representing a reduction in diversity in the area. Likewise, the recovery of *P. punctatus* may also warrant special attention. Rare species such as *A. obstetricans* and *P. punctatus* are more extinction-prone, and once they go locally extinct, they take longer to re-colonize than do common species (Harte 2003). Furthermore, theoretical work has shown how the loss of a single species from a guild can lead to further species loss, with those species lost being unable to

establish following reintroduction in some cases (Lundberg, Ranta & Kaitala 2000; Fowler & Lindström 2002), as well as considerable changes in the relative abundance of the remaining community members (Fowler 2005). However, an encouraging result from our study was that all other species sampled showed a recovery over the study period with an increase in the number of ponds inhabited in three cases (*R. LRE*, *H. arborea* and *B. bufo*).

While the best option is clearly to prevent the loss of natural breeding sites, this study shows that wetlands created as replacement sites can provide suitable alternative habitat. To further improve the success of these new ponds, additional measures have been implemented (Lesbarrères & Lodé 2000). Passages for amphibians were installed underneath the highway to reduce roadkills and increase gene flow between populations (Lesbarrères, Lodé & Merilä 2004), and terrestrial habitats have also been protected along the roadside to provide a terrestrial buffer zone (Marsh & Trenham 2001; Gibbons 2003). Overall, our data indicate that colonization rate is species- and site-specific, but that recovery of both species richness and diversity occurred in approximately 3 years (Petranka *et al.* 2003a). Additionally, we have shown that new ponds should be designed to provide a large area and a heterogeneous vegetation structure in order to quickly restore amphibian diversity (Oertli *et al.* 2002; Vignoli, Bologna & Luiselli 2007). Long-term monitoring will be necessary to distinguish human impacts from natural fluctuations (Pechmann *et al.* 1991) and to assess the long-term success of the restoration project with respect to site sustainability (Petranka *et al.* 2007) and population size (Pellet *et al.* 2007). Monitoring for at least 5 years will be required to assess demographic responses to site restoration because amphibians have significant population lags due to their stage-structure (i.e. eggs, tadpoles, juveniles, adults) and their sensitivity to site perturbations (Petranka *et al.* 2003b; Mattfeldt, Bailey & Campbell Grant 2009). Wherever possible, sampling should be carried out for several years before target ponds are destroyed and control ponds should be included in the restoration plans so that the background level of temporal fluctuation can be assessed. Although it is clear that local population recovery has taken place in this study, it is hoped that these results will be beneficial at a larger scale (Semlitsch 2002). Ultimately, species conservation and the maintenance of biodiversity can only be achieved if we understand the consequences of habitat change for amphibians (Gardner, Barlow & Peres 2007; Todd *et al.* 2009), we monitor regional and local species distributions and declines (Werner *et al.* 2007), and, most importantly, we assess the success of restoration efforts.

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References

Alford, R.A. & Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics*, **30**, 133–165.

Arntzen, J. & Teunis, S. (1993) A six year study on the population dynamics of the crested newt *Triturus cristatus* following the colonization of a newly created pond. *The Herpetological Journal*, **3**, 99–110.

Baker, J.M. & Halliday, T.R. (1999) Amphibian colonization of new ponds in an agricultural landscape. *Herpetological Journal*, **9**, 55–63.

Beebee, T.J.C. (1997) Changes in dewpond numbers and amphibian diversity over 20 years on chalk downland in Sussex, England. *Biological Conservation*, **81**, 215–219.

Berry, W.D. & Fieldman, S. (1985) *Multiple Regression in Practice*. Sage, Beverly Hills and London.

Berven, K.A. (1990) Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, **71**, 1599–1608.

Blaustein, A.R. & Kiesecker, J.M. (2002) Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters*, **5**, 597–608.

Burnham, K. P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, USA.

Crochet, P.-A., Chaline, O., Cheylan, M. & Guillaume, C.P. (2004) No evidence of general decline in an amphibian community of Southern France. *Biological Conservation*, **119**, 297–304.

Cushman, S.A. (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation*, **128**, 231–240.

Denton, J.S., Hitchings, S.P., Beebee, T.J.C. & Gent, A. (1997) A recovery program for the Natterjack toad (*Bufo calamita*) in Britain. *Conservation Biology*, **11**, 1329–1338.

Ficetola, G.F. & de Bernardi, F. (2004) Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation*, **119**, 219–230.

Ficetola, G.F., Padoa-Schioppa, E. & De Bernardi, F. (2009) Influence of landscape elements in riparian buffers on the conservation of semiaquatic Amphibians. *Conservation Biology*, **23**, 114–123.

Fog, K. (1993). Migration in the tree frog *Hyla arborea*. *Ecology and Conservation of the European Tree Frog* (eds H.P. Stumpel & U. Tester), pp.55–64. DLO: Institute for Forestry and Nature Research, Wageningen, The Netherlands.

Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, **29**, 207–231.

Fowler, M.S. (2005) Predicting community persistence based on different methods of community ranking. *Annales Zoologici Fennici*, **42**, 533–543.

Fowler, M.S. & Lindström, J. (2002) Extinctions in simple and complex communities. *Oikos*, **99**, 511–517.

Gardner, T.A., Barlow, J. & Peres, C.A. (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166–179.

Germano, J.M. & Bishop, P.J. (2009) Suitability of amphibians and reptiles for translocation. *Conservation Biology*, **23**, 7–15.

Gibbons, J.W. (2003) Terrestrial habitat: a vital component for herpetofauna of isolated wetland. *Wetlands*, **23**, 630–635.

Gibbons, J.W., Winne, C.T., Scott, D.E., Willson, J.D., Glaudas, X., Andrews, K.M., Todd, B.D., Fedewa, L.A., Wilkinson, L., Tsaliagos, R.N., Harper, S.J., Greene, J.L., Tuberville, T.D., Metts, B.S., Dorcas, M.E., Nestor, J.P., Young, C.A., Akre, T., Reed, R.N., Buhlmann, K.A., Norman, J., Croshaw, D.A., Hagen, C. & Rothermel, B.B. (2006) Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. *Conservation Biology*, **20**, 1457–1465.

Gilioli, G., Bodini, A., Baumgärtner, J., Weidmann, P. & Hartmann, J. (2008) A novel approach based on information theory to rank conservation strategies: an application to amphibian metapopulations. *Animal Conservation*, **11**, 453–462.

Harte, J. (2003) Tail of death and resurrection. *Nature*, **424**, 1006–1007.

Hecnar, S.J. & M'Closkey, R.T. (1996a) Amphibian species richness and distribution in relation to pond water chemistry in south-western Ontario, Canada. *Freshwater Biology*, **36**, 7–15.

Hecnar, S.J. & M'Closkey, R.T. (1996b) Regional dynamics and the status of amphibians. *Ecology*, **77**, 2091–2097.

Hels, T. & Buchwald, E. (2001) The effect of road kills on amphibian populations. *Biological Conservation*, **99**, 331–340.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. & Kuzmin, S.L. (2000) Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752–755.

Jaeger, R.G. (1994). Transect sampling. In *Measuring and Monitoring Biological Diversity: Standard Method for Amphibians*. (eds W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek & M.S. Foster), pp. 103–107. Smithsonian Institution Press, Washington, DC, USA.

Kentula, M.E., Brooks, R.P., Gwin, S.E., Holland, C.C., Sherman, A.D. & Sifneos, J.C. (1993) *An approach to Improve Decision Making in Wetland Restoration and Creation*. CRC Press, Boca Raton, FL, USA.

Kiesecker, J.M., Blaustein, A.R. & Belden, L.K. (2001) Complex causes of amphibian population declines. *Nature*, **410**, 681–684.

Kustler, J.A. & Kentula, M.E. (1990) *Wetland Creation and Restoration: The Status of the Science*. Island Press, Washington, DC, USA.

Lehtinen, R.M. & Galatowitsch, S.M. (2001) Colonization of restored wetlands by amphibians in Minnesota. *American Midland Naturalist*, **145**, 388–396.

Lesbarrères, D. & Lodé, T. (2000) La conservation des amphibiens: exemple d'aménagements autoroutiers. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, **22**, 37–48.

Lesbarrères, D. & Lodé, T. (2002) Influence de facteurs environnementaux sur la reproduction de *Rana dalmatina* (Anura, Ranidae): implications pour sa conservation. *Bulletin de la Société Herpétologique de France*, **104**, 62–71.

Lesbarrères, D., Lodé, T. & Merilä, J. (2004) What type of road underpass could potentially reduce amphibian road kills? *Oryx*, **38**, 220–223.

Lichko, L.E. & Calhoun, A.J.K. (2003) An evaluation of vernal pool creation projects in New England: project documentation from 1991–2000. *Environmental Management*, **32**, 141–151.

Loman, J. & Lardner, B. (2006) Does pond quality limit frogs *Rana arvalis* and *Rana temporaria* in agricultural landscapes? A field experiment *Journal of Applied Ecology*, **43**, 690–700.

Lundberg, P., Ranta, E. & Kaitala, V. (2000) Species loss leads to community closure. *Ecology Letters*, **3**, 465–468.

Maes, D. & Bonte, D. (2006) Using distribution patterns of five threatened invertebrates in a highly fragmented dune landscape to develop a multi-species conservation approach. *Biological Conservation*, **133**, 490–499.

Marsh, D.M. & Trenham, P.C. (2001) Metapopulation dynamics and amphibian conservation. *Conservation Biology*, **15**, 40–49.

Mattfeldt, S.D., Bailey, L.L. & Campbell Grant, E.H. (2009) Monitoring multiple species: estimating state variables and exploring the efficacy of a monitoring program. *Biological Conservation*, **142**, 720–737.

Meyer, A.H., Schmidt, B.R. & Grossenbacher, K. (1998) Analysis of three amphibian populations with quarter-century long time-series. *Proceedings of the Royal Society of London B Biological Sciences*, **265**, 523–528.

Mitsch, W.J. & Wilson, R.F. (1996) Improving the success of wetland creation and restoration with know-how, time, and self-design. *Ecological Applications*, **6**, 77–83.

Oertli, B., Auderset Joye, D., Castella, E., Juge, R., Cambin, D. & Lachavanne, J.B. (2002) Does size matter? The relationship between pond area and biodiversity *Biological Conservation*, **104**, 59–70.

Pavignano, I., Giacoma, C. & Castellano, S. (1990) A multivariate analysis of amphibian habitat determinants in north western Italy. *Amphibia-Reptilia*, **11**, 311–324.

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J. & Gibbons, J.W. (1991) Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science*, **253**, 892–895.

Pechmann, J.H.K., Estes, R.A., Scott, D.E. & Gibbons, J.W. (2001) Amphibian colonization and use of ponds created for trial mitigation of wetland loss. *Wetlands*, **21**, 93–111.

Pellet, J., Fleishman, E., Dobkin, D.S., Gander, A. & Murphy, D.D. (2007) An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation*, **136**, 483–495.

Petranka, J.W., Kennedy, C.A. & Murray, S.S. (2003a) Responses of amphibians to restoration of a southern Appalachian wetland: a long-term analysis of community dynamics. *Wetlands*, **23**, 1030–1042.

Petranka, J.W., Murray, S.S. & Kennedy, C.A. (2003b) Responses of amphibians to restoration of a southern Appalachian wetland: perturbations confound post-restoration assessment. *Wetlands*, **23**, 278–290.

Petranka, J.W., Harp, E.M., Holbrook, C.T. & Hamel, J.A. (2007) Long-term persistence of amphibian populations in a restored wetland complex. *Biological Conservation*, **138**, 371–380.

Pullin, A.S., Knight, T.M., Stone, D.A. & Charman, K. (2004) Do conservation managers use scientific evidence to support their decision-making? *Conservation Biology*, **119**, 245–252.

Ranta, E., Kaitala, V., Fowler, M.S., Laakso, J., Ruokolainen, L. & O'Hara, R. (2008) Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos*, **117**, 1907–1911.

Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D. & Frankham, R. (2003) Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation*, **113**, 23–34.

Ruokolainen, L., Lindén, A., Kaitala, V. & Fowler, M.S. (2009) Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology & Evolution*, **24**, 555–563.

Seigel, R.A. & Dodd . Jr, C.K. (2002) Translocations of amphibians: proven management method or experimental technique? *Conservation Biology*, **16**, 552–554.

Semlitsch, R.D. (2000) Principles for management of aquatic breeding amphibians. *Jounal of Wildlife Management*, **64**, 615–631.

Semlitsch, R.D. (2002) Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology*, **16**, 619–629.

Semlitsch, R.D. & Gibbons, J.W. (1988) Fish predation in size-structured populations of treefrog tadpoles. *Oecologia*, **75**, 321–326.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K. & Gibbons, J.W. (1996a) Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. *Long-term Studies of Vertebrate Communities* (eds M.L. Cody & J. Smallwood), pp. 217–248. Academic Press Inc, New York, USA.

Semlitsch, R.D., Schmiedehausen, S., Hotz, H. & Beerli, P. (1996b) Genetic compatibility between sexual and clonal genomes in local populations of the hybridogenetic *Rana esculenta* complex. *Evolutionary Ecology*, **10**, 531–543.

Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.

Snodgrass, J.W., Komoroski, M.J., Bryan, J.A.L. & Burger, J. (2000) Relationship among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology*, **14**, 414–419.

Stumpel, A.H.P. & Hanekamp, G. (1986). Habitat ecology of *Hyla arborea* in The Netherlands. *Studies in Herpetology, Proceedings of 3rd Meeting of S.E.H.* (ed. Z. Rocek), pp. 409–411. S.E.H., Prague.

Todd, B.D., Luhring, T.M., Rothermel, B.B. & Gibbons, J.W. (2009) Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *Journal of Applied Ecology*, **46**, 554–561.

Vasconcelos, D. & Calhoun, A.J.K. (2006) Monitoring created seasonal pools for functional success: a six-year case study of amphibian responses, Sears Island, Maine, USA. *Wetlands*, **26**, 992–1003.

Vignoli, L., Bologna, M.A. & Luiselli, L. (2007) Seasonal patterns of activity and community structure in an amphibian assemblage at a pond network with variable hydrology. *Acta Oecologica*, **31**, 185–192.

Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2007) Amphibian species richness across environmental gradients. *Oikos*, **116**, 1697–1712.

Zimmerman, B.L. (1994). Audio strip transects. *Measuring an Monitoring Biological Diversity: Standard Method for Amphibians* (eds W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek & M.S. Foster), pp. 103–107. Smithsonian Institution Press, Washington, DC, USA.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Multiple regression models for species richness.

Table S2. Multiple regression models for Simpson's inverse diversity index.

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