

Multi-scale effect of landscape processes and habitat quality on newt abundance: Implications for conservation

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Abstract

Recent studies in population dynamics suggest that landscape processes and habitat quality act at different scales on population abundances, but very few have modelled their simultaneous effects. However, at a time of large declines in natural populations, it is essential to understand such multivariate components. We tested the hypothesis that natural populations of palmate newts (*Triturus helveticus*) are affected on three scales: breeding patch (pond), habitat complementation (terrestrial cover), and metapopulation structure (density of ponds, surrounding populations). We conducted our survey in 130 ponds from southern France (Larzac) and analysed data with generalized additive models (GAM). Two main novel results emerge from these models: (1) the three landscape scales have significant effects on newt abundance, with more newts in deep, vegetated ponds, devoid of fish and surrounded by wooded areas and inhabited ponds; (2) the quality of the surrounding breeding patches is of primary importance in determining the abundance at core sites in a complex way: high abundances are associated positively with high densities of inhabited ponds, but negatively with the number of surrounding ponds. Deforestation, invasive species and abandonment of ponds all have negative impacts on the persistence of palmate newt populations. Future studies should encompass landscapes at different scales and incorporate the habitat quality in surrounding sites to better understand population dynamics and provide adequate conservation measures.

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1. Introduction

One of the main purposes of ecology is to know and understand the factors affecting the distribution of organisms (Dunning et al., 1992 and Tokeshi, 1999). The determinants of habitat selection are particularly varied in species that use different environments during their lifetime (Pope et al., 2000 and Resetarits, 2005). This is specifically the case in amphibian species, which exhibit complex life cycles (Duellman and Trueb, 1994) at three levels of influence (Pope et al., 2000 and Cushman, 2006) within a complex landscape matrix (Joly et al., 2001). The first level, the aquatic habitat is the place of breeding, egg laying and growth of branchiate offspring until metamorphosis (Duellman and Trueb, 1994 and Griffiths, 1996). At this scale, the presence of alien species (Bradford et al., 1994, Gamradt and Kats, 1996 and Knapp and Matthews, 1996), aquatic vegetation (Joly et al., 2001), water depth (Hecnar and M'Closkey, 1998) and pollutants (Bridges and Semlitsch, 2000) have been associated with the occurrence of amphibians. The second level, the landscape complementation occurs when

individuals move between habitats in the landscape to make use of non-substitutable resources (Dunning et al., 1992). In many amphibians, this is a characterisation of the environment occupied after the reproductive period, i.e. terrestrial habitats used for displacements, foraging, hibernation and estivation (Laan and Verboom, 1990, Guerry and Hunter, 2002, Houlahan and Findlay, 2003, Porej et al., 2004 and Hermann et al., 2005). The third level, the metapopulation structure (Hanski, 1998) is associated with the density of suitable breeding sites (Sjögren, 1991, Vos and Stumpel, 1995, Pope et al., 2000 and Joly et al., 2001). However, habitat quality can negatively affect pattern of distribution and thus mask metapopulation structures (Marsh and Trenham, 2001 and Resetarits, 2005). Despite this, the effect of the size of surrounding populations has been a neglected field in amphibian ecology and conservation. To our knowledge, only one study took this into consideration: this is an important factor because aquatic ponds differ in their attractiveness (Pope et al., 2000). Counting the number of waterbodies around a study pond, independently of the abundances in those ponds, is thus expected to bias our understanding of the effect of pond den-

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sity on abundance at each site (Marsh and Trenham, 2001) and lead to inefficient conservation measures. Occurrence is a good indicator of the large scale requirements of species, particularly in studying large geographical areas with regions differing in land use. When the habitat is a mosaic of suitable and unsuitable patches at the scale of the dispersion range of species, some ponds can produce very low numbers of offspring or function as sinks in receiving dispersing individuals from surrounding productive aquatic sites (Gill, 1978 and Perret et al., 2003). In this situation, abundance becomes a better tool than occurrence (Houlahan and Findlay, 2003).

Understanding why species abundance differs among sites is the first step towards conservation, particularly in metapopulations within fragmented landscapes (Hanski, 1998). Amphibians are considered to be bio-indicators of general environmental health because of their ecological requirements as they have a sensitive skin and are ectotherms that can use both aquatic and terrestrial components of the habitat (Collins and Storfer, 2003). Their decline is affecting species from all ecosystems on earth and is caused by a combination of factors, some of them still unknown (Alford et al., 2001, Blaustein et al., 2003, Collins and Storfer, 2003 and Beebe and Griffiths, 2005). One-third of amphibian species have recently been classified as threatened, exceeding the number of birds and mammals for which such global patterns are known (Stuart et al., 2004). Although global climate change is a likely factor at a world scale, this remains difficult to demonstrate (Collins and Storfer, 2003). In contrast, many smaller-scale stressors have been identified, such as abandonment and destruction of unused waterbodies (Dodd and Smith, 2003), recreational activities (Rodriguez-Prieto and Fernandez-Juridic, 2005), invasive species introduction (Knapp and Matthews, 2000 and Kats and Ferrer, 2003), and transformation of land-use for crop fields (Houlahan and Findlay, 2003). Although local, these factors are causing larger-scale declines because they are globally widespread.

Larzac limestone plateau in the supra-Mediterranean area of southern France is a traditional agricultural area. Given the nature of the soils, most of the agriculture relies on cattle, but crop fields exist at the bottom of the valleys. Although the calcareous structure of Larzac does not favour the natural retention of water, farmers have built small artificial cattle ponds, known locally as "lavagne". All these aquatic habitats have been colonized by a large number of amphibians, including newts (Gabrion et al., 1977). However, as with the changes occurring, at global (Tilman et al., 2001), European (Stoate et al., 2001) and Mediterranean (Pinto-Correia and Vos, 2002) scales, the apparently preserved Larzac has also suffered from many detrimental factors over the last thirty years. Although cattle ponds are not designed for fishing purposes, many of them have been stocked with ornamental fish species. Comparison of population studies conducted in the 1970s and in 2002 showed that many palmate newt populations disappeared because of the introduction of fish (Denoël et al., 2005). There is also a trend in the abandonment of ponds by farmers, which make the ponds less attractive by amphibians as they degrade and lose the ability to retain water. The artificial structure of most of the ponds allows the determination of the abundance of species and the acquisition of reliable data on their ecological requirements. We chose the palmate newt (*Triturus helveticus*) as a model system because it is present in a large number of sites in varied abundance and can be easily sampled.

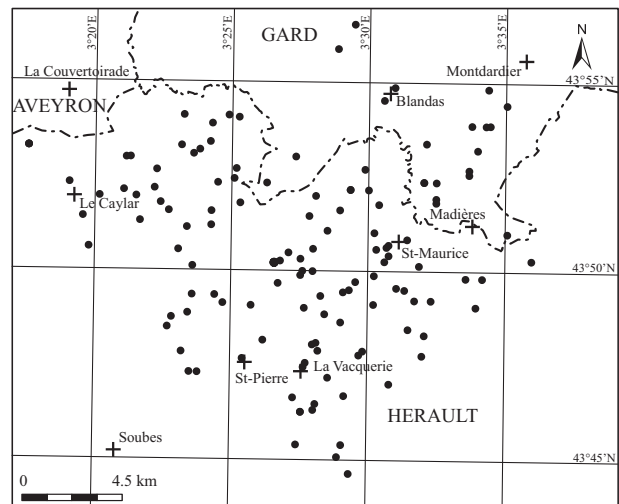


Fig. 1. Map of Southern Larzac showing the 130 core ponds (full circles), the limits between the departments of Hérault, Gard and Aveyron (dashed lines) and some of the villages (crosses).

Our aim was to provide a new perspective in the understanding of newt ecology, to discriminate among the main variables of the three scales of influence (pond, landscape complementation, and metapopulation) and to use abundance rather than presence in both core and surrounding ponds. Such an approach has been explored in frogs but never in caudate amphibians. However, it is of primary importance in order to apply efficient conservation measures to protect species and their aquatic and terrestrial habitats simultaneously. Our hypothesis is that all three levels influence newt abundance, and particularly that populations should be more abundant in habitats that we could classify as more suitable (i.e. deep, with abundant vegetation, without fish, with numerous suitable surrounding ponds, and availability of forestry cover).

2. Methods

2.1. Study sites and collecting procedures

We conducted our research in the Southern Larzac limestone plateau (south of the parallel at 48°85'; Hérault and Gard, France) (Fig. 1). This area is a mosaic of rural landscapes from crop field to forests. A total of 130 ponds were sampled during the peak of the breeding period of the palmate newt (*T. helveticus*), i.e. from the end of April to the end of May in the period 2002–2005. The collecting protocol consisted of making net sweeps in the ponds. We sampled all areas of the ponds following the circumference of circular ponds, or along parallel transects in the more rectangular ponds. We carried out dip-netting approximately every 50 cm, and curtailed the census when many dip-nettings failed to capture a newt. Only adult newts were considered in the determination of abundance. Ponds were sampled on average 1.9 times (SE = 0.1) and the highest recorded abundance at each site was used. As we used the same procedure at each site, the number of captured newts can be considered to be a reliable estimation of abundance.

2.2. Environmental features

We calculated the surface area (variable = area) and measured the maximum depth (depth) and the conductivity (cond) of each pond. We classified the

submerged aquatic vegetation cover (veg) into four categories: none, low (<10%), medium (10–50%), and high (>50%); the oxygen concentration at 10 cm under water surface (O_2 ,min) as low (0–6 mg/l) and high (>6 mg/l); the presence versus absence of fish based on direct capture (seining, dip-netting) and observations (fish); the ground as natural (no artificial cover) and artificial (with hard cover such as concrete); the surrounding environment (surround; at a few hundreds meters from core ponds) as agricultural (i.e., crop), open (open and bushy pastures), and forestry (open woods and closed forests). Although we measured pH, we did not use this variable in the model because we did not have this measure for all sites. That does not affect our results as pH had no effect on newt abundance in this subset of ponds (Spearman $R = 0.16$, $n = 77$, $P = 0.17$) and because the area does not include acidic ponds as it is the case in Northern Europe (see e.g. Beebee, 1983).

From topographic maps (Institut Géographique National, 1:25,000) and personal investigations in the field, we determined for each study pond: the elevation above sea level (alt), the number of surrounding ponds within 1260 m radius of each pond, which equates to an area of 500 ha when the pond is considered at the centre (ponds1260m), the number of ponds inhabited by palmate newts within 1260 m radius of each pond (pres1260m), and the abundance of newts within 1260 m radius of each pond (not including the core pond) (abund1260m). All these factors have been selected as potential predictors of newt abundance. Area, cond and abund1260m were log-transformed to compensate for their skewed distribution.

2.3. Modelling approach

We modelled the abundance of *T. helveticus* in using generalized additive models (GAM: Hastie and Tibshirani, 1990). These models are now frequently used in ecology (see applications in special issues: Guisan et al., 2002 and Lehmann et al., 2002a). The first published application was on modelling tree distribution in New Zealand (Yee and Mitchell, 1991). Their use is closely related to ecological theory and the study of response curve shapes (Austin and Graywood, 1994). Advanced applications are, for instance, found in the study of competitive interactions (Leathwick and Austin, 2001) or in reserve network selection (Ferrier et al., 2002). GAMs are a non-parametric extension of generalized linear models (GLM), which are themselves an extension

of classical multiple linear regression (MLR). The advantage of GLM and GAM over MLR is that they allow working with responses such as presence/absence data or abundances that do not follow a normal distribution. The advantage of GAM over GLM is that the response curves shapes are data-driven instead of being predefined by X or X2 terms. This new flexibility allows GAMs to be closer to the data, which is particularly useful in an ecological perspective. GAMs and GLMs can both employ quantitative and factor variables. GAMs have been used recently in other studies on amphibians (Joly et al., 2001 and Ray et al., 2002). The main reasons why we chose to use GAMs is that it allowed us to fit Poisson distributed data, such as counts, and that their response curves are not forced to be linear or quadratic.

We used the Generalized Regression Analysis and Spatial Prediction library (GRASP: Lehmann et al., 2002b) in Splus (Insightful) to select, validate and interpret models. First we tested the correlation between 12 candidate predictors in order to avoid high correlation ($r > 0.85$) between predictors (Table 1). A quasi-Poisson distribution was chosen to model *T. helveticus* abundance, because abundances are typically positive integer values that generally have an asymmetrical distribution. Variables were selected using a stepwise procedure, going in both directions, starting from a full model, where the significance of dropping or adding a variable was inferred from an *F*-test on changes in explained deviance. Quantitative variables were fitted with a smooth spline function using three degrees of freedom.

Goodness of fit was assessed by plotting observed abundances against predicted ones and calculating Spearman correlations. A randomization test was used to test this relationship by reselecting 500 times the model with a random association between the response (Y) and the predictors (Xs) (Manly, 2000). Randomized models that were removing all predictors were assigned a correlation of zero between observed and predicted abundances.

Predictor contributions were measured by looking in turn at the contribution of each variable within the model, expressed as the amount of variation on the linear predictor scale that one predictor can explain when all other variables are kept at fixed values. With GLMs and GAMs, models are first built in a linear form as a MLR and then transformed to suit the appropriate family of distribution (e.g. Poisson, binomial, Gaussian). The linear predictor scale is the scale of the model before this

Table 1. Spearman correlations coefficients between quantitative, binary and ordinal variables used in the GAM analysis

Variable	V1	V2	V3	V4	V5	V6	V7	V8	V9	V10	V11
V1: alt	–										
V2: logarea	–0.03	–									
V3: depth	0.04	0.62	–								
V4: logCond	0.18	–0.05	0	–							
V5: pres1260m	–0.08	–0.08	0.09	0.16	–						
V6: ponds1260m	–0.27	–0.13	–0.07	–0.08	0.64	–					
V7: logabund1260m	–0.07	–0.11	0.02	0.13	0.8	0.55	–				
V8: ground	–0.12	0.13	–0.11	0.1	0.11	0.15	0.16	–			
V9: veg	–0.08	0.01	–0.05	–0.2	–0.14	0.03	–0.2	–0.32	–		
V10: fish	–0.1	0.21	0.19	0.05	–0.05	0.01	–0.08	–0.23	0.3	–	
V11: O_2	0.02	0.01	–0.12	0.34	–0.04	–0.14	0.06	0.15	–0.06	–0.07	–

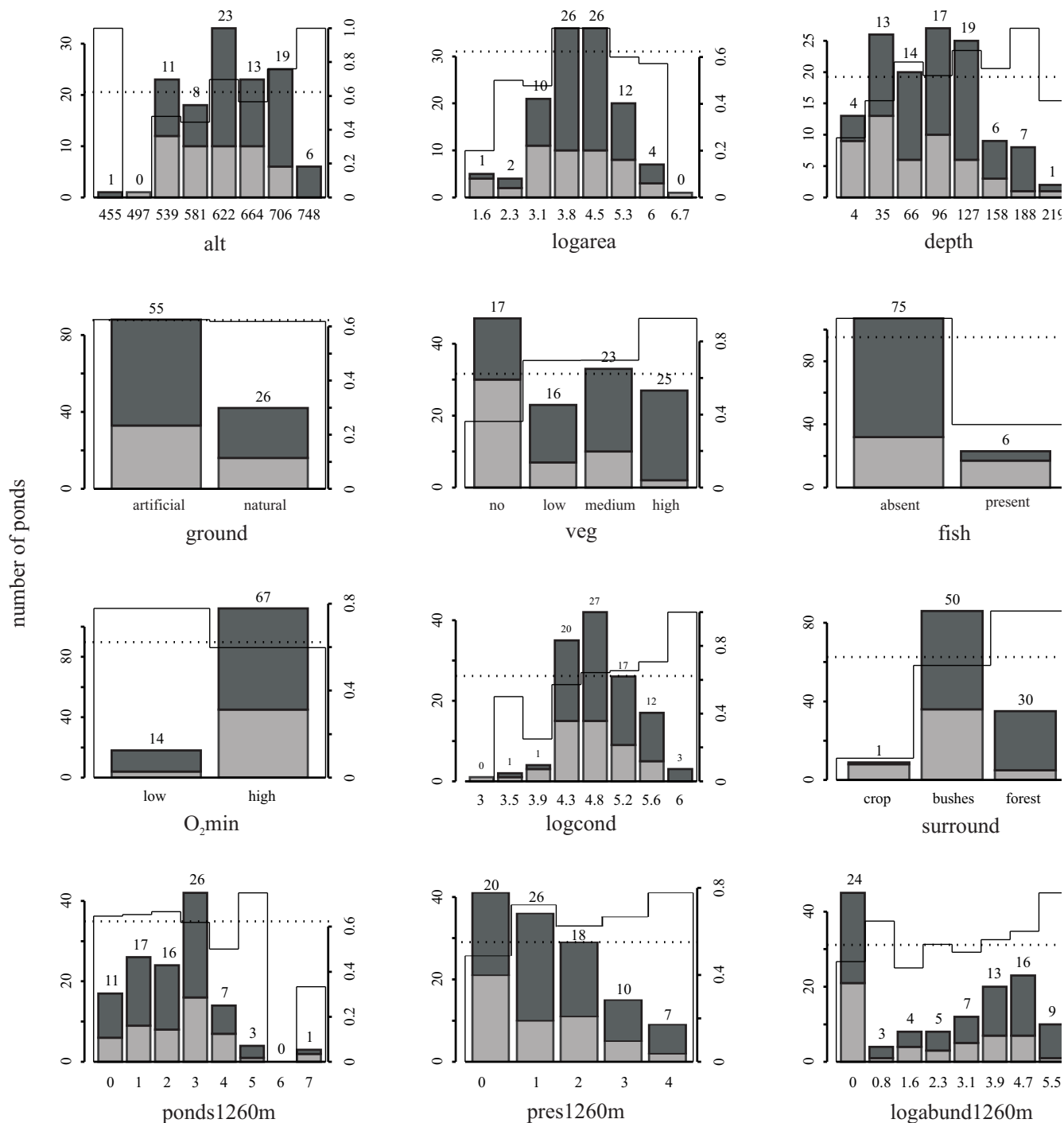


Fig. 2. Histograms of 12 candidate variables showing, in dark, the proportion of each bar occupied by *T. helveticus*. The number of occupied ponds is written on the top of each bar. Y-left axis: counts, Y-right axis: proportions. The plain line is the ratio between occupied and unoccupied ponds within each bar and the dashed line corresponds to the overall mean proportion of occupied ponds. The altitude is expressed in m, the pond area (log values) in m², the water depth in cm, and the conductivity (log values) in $\mu\text{S}/\text{cm}$.

transformation. The contribution of each predictor against the response was calculated as a measure of variable potential contribution on their own.

Legendre and Fortin (1989) rightly reminded ecologists that spatial structure is inherent to any ecological pattern. Legendre and Legendre (1998) explained how spatial structures originate in two different ways. Spatial dependence implies that the structure comes from underlying explanatory environmental variables, whereas spatial autocorrelation is assumed to result from some processes involving the response variable only. As stated by Liebhold and Gurevitch (2002), modern ecology tends to include spatial autocorrelation into models instead of ignoring or avoiding it. Here, we used autoregressive terms inspired from Leathwick (1998), namely

the abundance and the number of occupied ponds in a given neighbourhood. As a diagnostic, spatial autocorrelation was tested on the response variable and on the residuals of the model with a Moran's *I* statistics (ArcGIS, ESRI; Wagner and Fortin, 2005).

Interaction terms were tested by building a regression tree on the residuals in order to identify possible interactions (Maggini et al., in press). This approach allows taking advantage of the fact that regression trees can model interactions. The idea is to keep using the appealing smoothed and additive response curves of GAMs, and simply to test for interaction in the residuals. If interactions are found, they can be transformed into one single factor variable that is added to the original GAM model.

3. Results

The histograms of 12 candidate predictors (Fig. 2) give the distribution of the data along each environmental quantitative and factor predictors at the three levels of investigation; namely breeding sites (alt, logarea, depth, ground, veg, fish, O₂min, logcond), landscape (surround) and metapopulation (ponds1260m, pres1260m, logabund1260). The distribution of observations is well spread across each variable with no evidence of outliers.

Correlation between candidate quantitative predictors was low, except between logabund1260m

and pres1260m ($r = 0.80$) (Table 1). The stepwise procedure selected a model with eight predictors (Fig. 3). Logarea, logcond, and O₂min did not have a significant effect on the abundance of *T. helveticus*. In contrast, abundance increased with depth and number of *T. helveticus* presences within a 1260 m radius. It decreased, however, with *T. helveticus* abundance and the number of ponds within a 1260 m neighbourhood. The abundance of *T. helveticus* was also higher on artificial grounds, high vegetation cover, in the absence of fish, and in forested land cover. All these eight predictors were significantly contributing to the model according to an analysis of variance in which each term was drop-

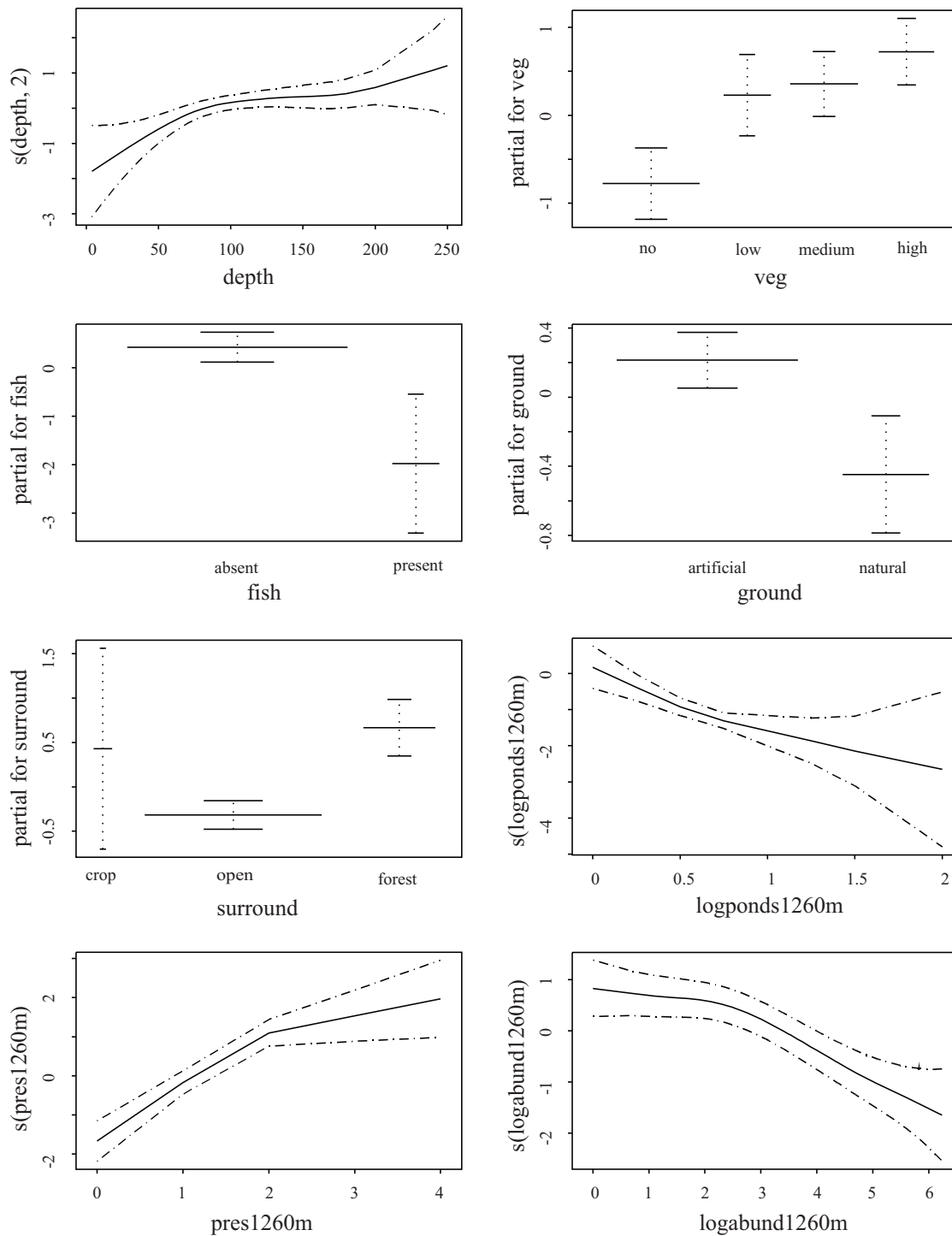


Fig. 3. Response curves of the abundances of *T. helveticus* to the environmental variables selected by the generalized additive model (center lines). The y-axes are based on partial residuals and indicate the relative influence of each explanatory variable on the prediction. Distance between the lower and upper curves indicates two times the point-wise standard errors for each curve or factor level. The length of the central line in discrete variables is proportional to the number of ponds.

Table 2. Analysis of variance (ANOVA) of selected model

Variable	df	Deviance	F	P
Model	19	12,188		
s(depth, 3)	3	-1026	6.48	<0.001
s(logponds1260m, 3)	3	-637	4.1	<0.01
s(abund1260, 3)	3	-1285	8.49	<0.001
s(pres1260m, 3)	3	-868	5.69	<0.05
Ground	1	-381	7.22	<0.01
Veg	3	-1009	6.44	<0.001
Fish	1	-768	14.06	<0.001
Surround	2	-723	6.95	<0.05

Number of degrees of freedom used (df), amount of deviance explained (or lost), F-statistics obtained when dropping a term from the full model (F), and related P -value (P).

ped in turn from the selected model and in which the change in explained deviance was tested (Table 2). The interaction factor did not contribute significantly to the model.

A significant spatial autocorrelation ($P < 0.05$) was found on the response (species abundance), but was no longer significant on the residuals of models including or excluding autocorrelative terms. No corrections were necessary on the model for the potential effect of spatial-autocorrelation as this is necessary only when autocorrelation is still present on model residuals (Wagner and Fortin, 2005).

Model validation presented a positive correlation of $r = 0.78$ between observed and predicted abundance. This correlation was confirmed with a randomization test proving that such correlation can be found in less than 95% of cases when the relationship between Y and X s is randomized (Fig. 4). The presented model resulted from a stepwise selection and was validated because of its very interesting ecological patterns. However, one should not forget that with many available predictors, as in this case, there are always other models that could satisfy the statistical requirements.

Finally, the contributions of selected predictors (Fig. 5) show that depth, vegetation cover and the

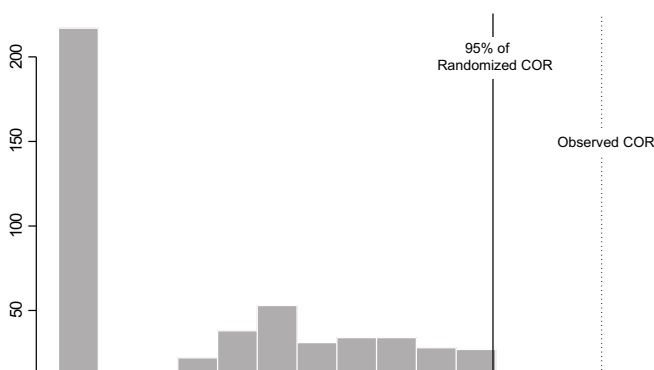


Fig. 4. Validation by a randomization test reselecting 500 times the GAM model with a random association between the response (Y) and the predictors (X s), and by recalculating the resulting correlation between observed and predicted abundances. Randomized models that were removing all predictors were assigned a correlation of zero between observed and predicted abundances.

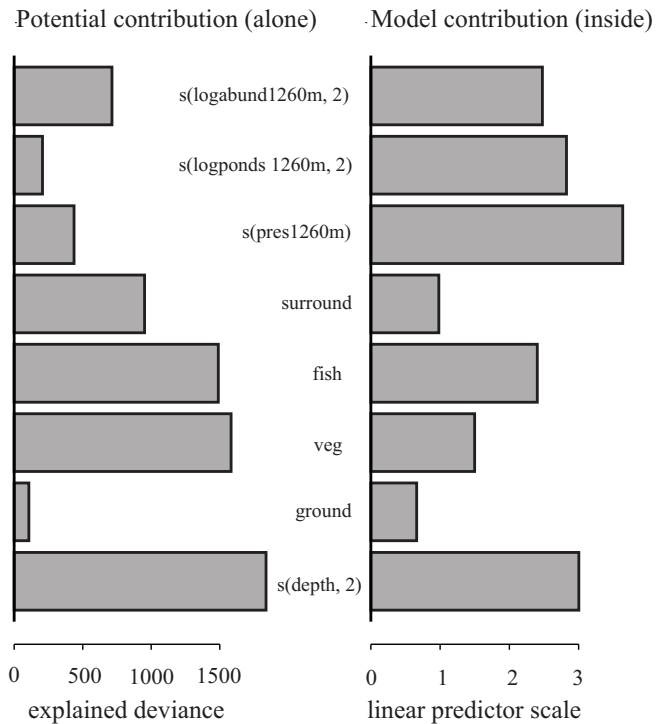


Fig. 5. Potential and model contributions from *T. helveticus* abundance model.

presence of fish had the highest potential in single-variable models. The most influential variables within the selected model were the total number of sites in a 1260 m radius, the depth, and the number of sites with *T. helveticus* presence. This also reveals an important discrepancy between single-variable and multi-variable contributions, especially for the three neighbourhood variables. This discrepancy is generally explained by the new equilibrium found between predictors in complex models.

4. Discussion

In integrating terrestrial and aquatic variables within full landscape coverage, and analysing them jointly in a GAM model, we stressed the importance of several predictors of newt abundance. They belong to three scales of influence: breeding site, landscape complementation and metapopulation. Water depth, abundance of aquatic vegetation and the presence of fish were the main single factors, but the surrounding terrestrial environment, the structure of the pond, and the presence of other nearby ponds also played a significant role. Specifically, the variables associated with the metapopulation structure were primary predictors of the model. However, the effects of pond density varied accordingly to their quality in terms of suitability for newts. These results offer new perspectives on the understanding of amphibian requirements and metapopulation dynamics, and consequently on adequate conservation measures.

4.1. Breeding site (pond)

Introductions of alien species are a major threat for biodiversity through competition, predation or alteration of the habitat and food web (Kiesecker, 2003). Native organisms are particularly vulnerable because they have not co-evolved with invasive species and consequently have not evolved antipredator behaviours (Kats and Ferrer, 2003). Pond-breeding

amphibians suffer from the introduction of fish (Knapp and Matthews, 2000 and Nyström et al., 2001), crayfish (Gamradt and Kats, 1996), reptiles (Moore et al., 2004) and other species of amphibians (Kiesecker and Blaustein, 1998). In most cases, the disappearance or decrease in population size have been recorded following fish stocking. In this study, alien fish were found in a fifth of the ponds. These ponds were created to provide water for cattle but, since the 1980s, local people started introducing fish for decorative purposes or as bait. The presence of fish was considered one of the three main predictors of newt abundance. Although present in a quarter of ponds containing fish, newts were never numerous in such habitats. This confirms results from Denoël et al., 2005 and Crochet et al., 2004 who found that palmate newts disappeared in most ponds stocked with fish. The main fish species involved in Larzac were golden fish (*Carassius auratus*), but some ponds also contained mosquitofish (*Gambusia affinis*), pumpkinseed sunfish (*Lepomis gibbosus*), tench (*Tinca tinca*), and minnow (*Phoxinus phoxinus*). Although most of the fish species are small-sized, their effect on natural populations can be as detrimental as that of large predatory species. *C. auratus* and *G. affinis* were documented to forage on the eggs or larvae of newts and salamanders (Gamradt and Kats, 1996 and Monello and Wright, 2001). The palmate newt is particularly affected because of its small-size and because it breeds and lays eggs in water.

Water depth and the abundance of aquatic vegetation are recognized predictors of the presence and abundance of most species of caudates (Joly et al., 2001), although some species are also known to select shallow (Beja and Alcazar, 2003) and less vegetated ponds (Lecis and Norris, 2003). Palmate newts in Larzac fit these predictions selecting deep and vegetated ponds. In the supra-Mediterranean environment, this is particularly advantageous because shallow ponds dry during summer and are thus hostile habitats for newt larvae. Aquatic vegetation offers shelter for newts against predators, but also for their invertebrate prey (Griffiths, 1996). Newts also wrap their eggs in the vegetation, which protect them from predation (Miaud, 1994). This may explain the importance of vegetation in sustaining large newt populations. Ponds with artificial bottoms were also preferred, probably because they may retain water during all the period of reproduction and larval development (Griffiths, 1996). Newts were present in a large spectrum of conductivity values, from 39 to 634 $\mu\text{S}/\text{cm}$, as previously found in Larzac (Gabrion et al., 1978) and in the United Kingdom (Beebee, 1983), but this variable had no effect on palmate newt abundance.

4.2. Habitat complementation (terrestrial habitat)

Pond-breeding amphibian species differ in their preference for terrestrial habitats. For many of them, forests are an important resource for hibernation, foraging and migrations (Guerry and Hunter, 2002, Houlihan and Findlay, 2003, Porej et al., 2004 and Hermann et al., 2005). These areas are of primary importance particularly through the availability of terrestrial refugia (e.g. logs) as shown in the smooth newt *Triturus vulgaris* (Marnell, 1998). In Larzac, the terrestrial landscape significantly affected the abundance of palmate newts, with the largest populations occurring in forested areas. Although palmate newts are well adapted to a large variety of habitats found in open fields far from forested areas, these results show the importance of forests in sustaining large populations. Fol-

lowing metamorphosis palmate newts live on land apart for short periods when they return to water to breed (Griffiths, 1996). Terrestrial buffer zones around breeding sites are thus essential to allow amphibians to complete their life cycle (Semlitsch, 1985 and Schabetsberger et al., 2004). Although previous studies reported that crops are negatively associated with newts (see e.g. Joly et al., 2001), we did not find higher abundances of newts in pasture compared with crop areas. This similarity may come from the lower use of chemicals in calcareous lands (e.g. almost no nitrates were found in Larzac ponds, which is very different from more intensively used agricultural areas: Denoël, 2004).

4.3. Metapopulation structure (pond and population distribution)

Habitat fragmentation, such as pond isolation in pond-breeding amphibians, has been suggested as a cause of decline (Dodd and Smith, 2003). This is based on metapopulation theory, which predicts that the persistence of populations in a patch is favoured by the presence of other nearby populations (Harrison, 1991, Wiens, 1997 and Hanski, 1998). In support of this hypothesis, high pond density favours the persistence of several species of amphibians (Sjögren, 1991, Vos and Stumpel, 1995, Ficetola and De Bernardi, 2004 and Porej et al., 2004). In newts, including *T. helveticus*, Joly et al. (2001) found similar results between site occupancy and the density of ponds, but they did not consider abundance. In contrast to these studies, we found that the higher the pond density, the lower the abundance of newts. However, this was without incorporating an estimation of the quality of the surrounding sites. Not all sites are equal and many of them may not be suitable for newts (e.g. because of predator species or shallow water depth: see e.g. Resetarits, 2005). Taking into account the density of ponds inhabited by newts, the pattern radically changes and follows the predicted direction, i.e. more newts when there are many surrounding ponds with newts. These results show that in a system with several potentially suitable aquatic habitats, i.e. occupied by newts, populations can reach large sizes. Pope et al. (2000) found a similar effect in leopard frogs (*Rana pipiens*) in surrounding ponds when terrestrial habitats were suitable. Similarly, Resetarits (2005) found that gray treefrogs (*Hyla chrysoscelis*) selected ponds in areas with the highest proportion of suitable ponds.

Despite this, we found that at very high newt abundance in surrounding ponds, the abundance at a given pond decreased. This unexpected result let us formulate the hypothesis that habitat quality could be of higher importance than connectivity in terms of abundance. Ponds with the highest abundances of newts were surrounded by suitable terrestrial habitats and were devoid of fish. Such areas most probably offer good conditions for both the aquatic and terrestrial life stages of the newts. We also hypothesize that newts may exhibit site tenacity in these ponds, which would also attract newts from nearby sites (Gill, 1978, Joly and Miaud, 1989 and Perret et al., 2003). Newt abundance in these peripheral sites is thus expected to decrease with the increase of attractiveness in the suitable ponds. Field monitoring and further experiments are needed to test this hypothesis, but it is not an easy task given the small size of palmate newts. However, our results offer new perspectives in conservation biology and suggest that more work should be done to determine the population dynamics in such systems. These efforts would help to clarify the relative role of the different variables. Specifically, the apparent

difference in the relative importance of variables, depending on whether they are considered separately or together, needs further investigation.

Generally speaking, although palmate newts prefer a habitat matrix including high densities of inhabited breeding sites, which can provide colonizers, habitat quality is likely to be more important than connectivity when such suitable sites are present.

4.4. Implications for conservation

Both terrestrial and aquatic habitats are essential features enabling palmate newt populations to persist. Newt abundance depends on a number of factors. Newts are more numerous in good quality habitat, i.e. no fish, vegetated and deep ponds surrounded by forested areas and suitable aquatic sites. They are favoured by agricultural practices that increase the number of available aquatic sites in such a dry environment. On the other hand, agriculture is responsible for opening the landscape, which has decreased the availability of suitable terrestrial habitats. However, the most detrimental factor is the introduction of invasive alien species. If fish introductions are not stopped in the near future, we predict that almost all the ponds from Larzac may suffer newt population losses. Comparisons between data from the 1970s and the present show that several newt populations have disappeared (Denoël et al., 2005). Together with the detrimental factors highlighted in the present study, it is clear that there is a local decline of amphibian populations in Larzac. Although pond occupancy can show interesting patterns (Crochet et al., 2004), abundance remains the most straightforward variable to characterise the status of populations.

Our study highlights the necessity of integrated landscape research for conservation purposes (Cushman, 2006). To protect core habitats, it is also of primary importance to apply conservation measures to the surrounding environment. Specifically, maintaining high quality habitats around core sites, such as additional suitable breeding patches (i.e. not only potential sites as not all are suitable), is an essential prerequisite for the persistence of natural newt populations.

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