

# Niche position, but not niche breadth, differs in two coexisting amphibians having contrasting trends in Europe

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## ABSTRACT

**Aim** We explored general habitat-related explanations (niche breadth and niche position) to the contrasting status of two amphibian species that have largely overlapping ranges and habitats – the rare and declining crested newt (*Triturus cristatus*), and the more common smooth newt (*Triturus vulgaris*). These closely related and ecologically similar species provide an excellent opportunity to study those methodologically challenging hypotheses, and this is the first such study on amphibians.

**Location** Denmark.

**Methods** We derived multivariate habitat models from 27 characteristics of 210 ponds and their surroundings, and their occupation by newts. In addition to the model performance, niche breadths were compared using the mean beta diversity of amphibian communities in the presence of each newt species.

**Results** For each newt species, the habitat models comprised three variables and correctly classified 74% of observations. Diverse invertebrate fauna (prey base) and shorter distances to other ponds inhabited by conspecifics were positive for both species, while the surrounding habitat (notably dry grasslands with forests) was important for the crested newt and the sediment type of the pond for the smooth newt only. Beta diversity of the amphibian communities of occupied ponds did not differ between the two newt species. Hence, in an area of frequent coexistence, habitat requirements of the species differed in key variables, not in the extent of specialization.

**Main conclusions** Our study supported the niche position rather than the niche-breadth hypothesis of rarity. We suggest that the rarity and/or continuing decline of the crested newt is related to the degradation of (semi)natural terrestrial habitats around suitable water bodies in Europe. Consequently, special restoration of such habitats has a high potential for the recovery of this rare species, while general pond management appeared more beneficial for the common smooth newt.

## Keywords

*Caudata*, conservation management, habitat degradation, habitat requirements, rarity, threatened species.

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## INTRODUCTION

Understanding the reasons for the rarity of some species is of obvious relevance for biodiversity conservation. One of the most general patterns of rarity (and for macroecology in general) is that species having small ranges also tend to be

locally rare – a tendency still insufficiently explained (Lawton, 1993). In this document, we explore two possible explanations to that relationship and their population restoration implications for a pair of amphibian species.

Mechanisms that might produce the abundance-range size relationship include several types of research artefacts, differing

population processes and two habitat-related explanations (Gaston *et al.*, 1997). The latter are (1) the niche-breadth hypothesis and (2) the niche-position (or habitat availability) hypothesis. According to (1), species attaining large geographical distributions and occurring at high local densities are capable for that because they occupy a broader range of habitats and exploit diverse environmental conditions and resources (Brown, 1984). According to (2), abundant species use resources that are common in the particular area and time, while rare species utilize locally scarce and restricted resources (Gaston, 1994; Gaston *et al.*, 1997).

As a contemporary pattern, the habitat-related explanations are not mutually exclusive (Heino, 2005): one can easily imagine a wider niche increasing habitat availability for a species (Gaston *et al.*, 1997) or the rarest species being highly specialized to rare resources and conditions. However, by stressing different evolutionary processes, these explanations affect our understanding of community structure and conservation strategies. The niche-breadth hypothesis highlights the specialization process; notably that species tend to specialize simultaneously in different dimensions of their multidimensional niche (Brown, 1984). The niche-position hypothesis rather includes the idea of niche conservatism (Wiens & Graham, 2005), which means that species carry their historically evolved habitat requirements in a dynamic world – so their distribution follows habitat availability in a particular time period. For conservation, niche-breadth hypothesis implies great difficulties with maintaining or creating conditions for viable populations of rare (highly specialized) species in the human-dominated world – unless these species adapt to new conditions. If niche-position hypothesis holds, habitat restoration is a more promising approach even in relatively small areas.

Relevance of these hypotheses to the real-world situations remains debatable. While a narrow niche has been an intuitively appealing explanation and is supported by large-scale studies measuring it in a very general way (Cofre *et al.*, 2007), detailed studies on various taxa have rather supported the niche-position hypothesis (Seagle & McCracken, 1986; Shenbrot, 1992; Gaston, 1994; Thompson & Ceriani, 2003; Heino & Soininen, 2006; but see Brändle & Brandl, 2001). A major source of confusion is the methodology to distinguish between the hypotheses. In particular, niche differences may appear as artefacts if the species compared occupy different areas or are sampled in unequal numbers (Williams, 2005) or exclude each other competitively from parts of their fundamental niches in nature (Keddy, 1989). In turn, laboratory conditions are much simplified and 'similar' niches there may miss complicated requirements (Clark *et al.*, 2007). Hence, theoretically, closely related rare and common species should be studied in areas where they co-occur in similar numbers (Williams, 2005). Such situations are uncommon in the real world, but here we describe one example.

We compare habitat requirements of the threatened crested newt (*Triturus cristatus*) and the common smooth newt (*Triturus vulgaris*) in a region of their frequent coexistence,

in the same ponds in Denmark. Our aim was to detect niche differences indicative of the contrasting population trends of the species and, thereby, of the habitat restoration potential – as the crested newt is a protected species (listed in the Annexes II and IV of the EU Habitats Directive, 92/43/EEC), but only limited conservation work has taken place (Edgar & Bird, 2006). We use multi-scale multivariate habitat modelling improved with two aspects of management relevance – the importance of immigration for pond occupancy and the efficacy of current conservation management. Approximately 4000 ponds have been dug and restored for amphibians since 1989 in Denmark – half of them for a general improvement of amphibian habitats, and the rest for five rare and endangered species, but not for the newts studied by us (Fog, 1997). We therefore test whether, after the species' other requirements have been taken into account, the occupancy of managed ponds differs from that of natural ponds. Combined with the results of the niche analysis, this finding indicates whether an efficient restoration of crested newt habitats should follow a more species-specific approach than presently (Stumpel, 2004).

## METHODS

### Study species

The crested newt and the smooth newt are mostly aquatic amphibians, with overlapping timing of seasonal and daily activities; they often inhabit the same landscapes and water bodies throughout their distribution ranges (Zuiderwijk, 1986; Griffiths & Mylotte, 1987; Skei *et al.*, 2006; van Buskirk, 2007). The crested newt is the larger species and may predate on the larvae of the smooth newt (Griffiths *et al.*, 1994), but in general the interspecific interactions are weak because of the differences in their feeding habits, microhabitats or diel activity pattern (Griffiths & Mylotte, 1987; Dolmen, 1988). The crested newt populations are in decline in many European countries (Edgar & Bird, 2006), while the smooth newt is widespread and locally abundant (Griffiths & Mylotte, 1987; Dolmen, 1988; Fog *et al.*, 1997). The proposed factors for the declines of the crested newt are habitat-related: the loss of ponds, habitat fragmentation, introduction of fish and changes in agricultural systems (Joly *et al.*, 2001; Edgar & Bird, 2006; Skei *et al.*, 2006). Yet, the same processes have not affected the coexisting smooth newt to such an extent.

### Study area and field methods

We performed the study in central and southern Denmark – an area situated very similarly with respect to the geographical ranges of the species (cf. the possible range-position artefact; Gaston *et al.*, 1997). We derived habitat models from a dataset of 27 ecological characteristics of 210 ponds and their surroundings. One-hundred ponds had been managed by the conservation authorities (since 1992); the rest being natural depressions or water bodies created by local people (for cattle or hunting; marl or peat). The ponds were 0.5–3 m deep and

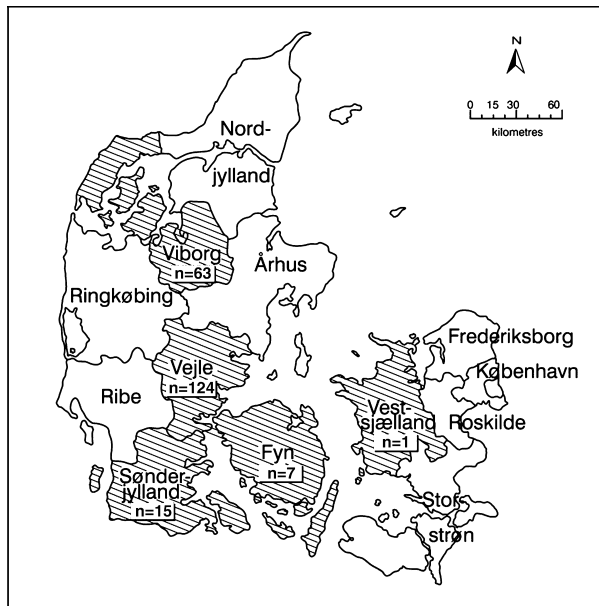


Figure 1 The study counties in Denmark (striped) with the numbers of investigated ponds.

8–11,550 m<sup>2</sup> in size (median 456; quartile range 178–947 m<sup>2</sup>). They were situated in the four main landscape types of Denmark: forest, semi-natural habitats, mosaic landscapes with extensive agriculture and intensively managed agricultural land. Geologically, the area is a moraine landscape with clay and sandy underground.

The fieldwork was carried out by 10 herpetologists in late June–July 2004 and 2005 in most of the counties, and in August 2005 in Sønder-Jylland (Fig. 1). Data collection was carefully standardized and simplified. We used a standard dip-netting of larvae (Skei *et al.*, 2006) as the main method for detecting amphibians. In each pond, 10 dip-net sweeps were made covering important microhabitats for newts. Accidentally, adults were caught as well: smooth newts in 32 and crested newts in 19 ponds. Due to the single visit to each pond, random effects in the number of caught individuals were probably large and we used only presence–absence for analyses. The ‘absences’ may include some undetected presences, but not extensively: for eight ponds, sampled three times for checking the reliability, the final results (seven presences and one absence of larval newts) were already obtained with the first visit. In turn, because of our focusing on larvae (i.e. breeding), the ‘presences’ probably do not contain many marginal habitats, which might confound the niche determination (Pulliam, 2000; Hirtzel & Le Lay, 2008).

Dip-netting also provided data on other amphibian species for species-richness analyses and – as a ‘by-catch’ – on invertebrates to characterize the newts’ food-base diversity (Griffiths & Mylotte, 1987). For the latter, 15 invertebrate taxa to be registered were pre-defined (Table 1). In a thoroughly studied sub-sample, the number of taxa present was well related to the total invertebrate abundance (Fig. 2). We established the presence of fish, using the combined data of

visual observation, dip-netting and information from local people.

Altogether, 18 aquatic and 11 terrestrial features of potential importance to larval and adult newts were assessed for each pond, including eight landscape-variables measured from the Danish base map (Table 1). Instead of fluctuating water-chemistry variables, we used the more stable geological (sediment), physical (water transparency/colour) and biological (vegetation structure and invertebrate diversity) parameters well related to water chemistry (see Brönmark & Hansson, 2005). Land-cover type was studied within 50-m radius from each pond – a typical home-range migration distance of adult crested newts (Jehle, 2000; Müllner, 2001). We distinguished meadows and dry grasslands, for the former are usually influenced by fertilization while dry grasslands have remained quite natural in Denmark. To characterize potential immigration sources, we estimated the number of other ponds nearby for four distance classes up to 800 m (the maximum migration distance of juvenile crested newts; Kupfer & Kneitz, 2000) as well as the distance to the nearest pond occupied by conspecifics.

### Data analyses

We used multivariate habitat modelling and species co-occurrence patterns to explore the niche differences between the newt species. Given their co-existence, we expected some requirements of the species to overlap but, to support the niche-position hypothesis, differences in other key variables should correspond to environmental degradation in Europe. We addressed the challenging niche-breadth hypothesis (Gaston *et al.*, 1997) by using two approaches: (1) habitat model performance – if the models largely explain the abundance (i.e. essential requirements are included), relatively poorer performance of the common-species model and a wider set of variables included in it would indicate a wider niche (Tsoar *et al.*, 2007); and (2) the relative beta-diversity in the occurrence sites of each species (Fridley *et al.*, 2007).

Before model building, we used chi-squared tests to check whether the presence of fish was a major limitation for newt occurrence, as shown in several studies (Joly *et al.*, 2001; Denoël *et al.*, 2005; Skei *et al.*, 2006); after the confirmation (see Results), we omitted the ponds hosting fish from further analyses. To improve replication quality, we also omitted closely neighbouring ponds by selecting randomly one pond from each pair or cluster where the between-pond distances were  $\leq 200$  m (the average migration distance of juvenile crested newts; Kupfer & Kneitz, 2000).

With the final set of 140 ponds, we built multiple logistic regression models according to the procedure of Hosmer & Lemeshow (1989): (1) performed univariate analyses for each of the 27 independent variables; (2) built preliminary multivariate models, which included the potentially important variables according to the univariate analyses; and (3) omitted non-significant and/or redundant variables (Table 2) considering their biological meaning and large differences in

**Table 1** Variables measured in the aquatic and terrestrial habitat of the crested newt (*Triturus cristatus*, T.c.) and the smooth newt (*Triturus vulgaris*, T.v.)<sup>a</sup>.

Acronym	Description of the variable	n	P-value	
			<i>Triturus cristatus</i>	<i>Triturus vulgaris</i>
Area	Total area of the pond (m <sup>2</sup> )	140	0.573	0.188
Management	Unmanaged vs. restored/new-dug pond	140	0.038	< 0.001
Shallow	Mean width of shallow (up to 50 cm) water zone in the pond (m) measured from four cardinal edges	140	0.137	0.540
Buffer	Mean width of uncultivated land around the pond (m) measured from four cardinal edges	140	0.011	0.088
Slope	Mean slope (°) of the four cardinal banks of the pond	140	0.478	0.114
Sediment	Type of pond bottom (four types)	140	0.050	< 0.001
Water	Transparency or colour of the water (four types)	140	0.024	< 0.001
Grazing	Presence of grazing around the pond	140	0.575	0.627
Land cover < 50 m	Main land cover within 50 m: forest (eight types)	140	< 0.001	0.249
Near. forest*	Distance from the pond to the nearest forest (m)	133	0.209	0.882
Near. pond*	Distance from the pond to the nearest pond (m)	133	0.896	0.979
Ponds < 100 m*	Number of ponds within 100 m around the pond	133	0.092	0.194
Ponds 100–200 m*	Number of ponds within 100–200 m around the pond	133	0.407	0.482
Ponds 200–500 m*	Number of ponds within 200–500 m around the pond	133	0.135	0.483
Ponds 500–800 m*	Number of ponds within 500–800 m around the pond.	133	0.827	0.779
Near. T.v. pond*	Distance to the nearest pond with <i>Triturus vulgaris</i> (km)	133	n.a.	0.063
Near. T.c. pond*	Distance to the nearest pond with <i>Triturus cristatus</i> (km)	133	0.007	n.a.
Shading	% of the water-table of the pond under shadow	120	0.581	0.202
Vege > 1 m	% of pond area occupied by > 1 m high vegetation	137	0.035	0.026
Vege < 1 m	% of pond area occupied by < 1 m high vegetation	137	0.223	0.423
Floating	% of pond area occupied by floating vegetation	137	0.224	0.106
Submerged	% of pond area occupied by submerged vegetation	137	0.726	0.364
Open	% of water-table without plant cover	137	0.857	0.077
Algae	Presence/absence of floating macro-algae in the pond.	140	0.455	0.644
Invert.	No. invertebrate groups per 10 dip nets. 15 taxa: Turbellaria, Hirudinea, Ephemeroptera, Odonata, Zygoptera, Heteroptera, Trichoptera, Coleoptera, Megaloptera, Chironomidae, Gastropoda, Bivalvia, <i>Gammarus</i> , <i>Asellus</i> , <i>Argyroneta</i>	140	0.023	< 0.001
Fish	Presence of fish in the pond.	210	0.001	< 0.001
Bird	Presence of nesting or foraging birds in the pond	140	0.30	0.220

<sup>a</sup>The variables marked with asterisk (\*) were measured from the digital base map of Denmark; significance levels are from univariate logistic regression (n.a. – not applicable). See Table 4 for the categories of Sediment, Water and Land cover < 50 m.

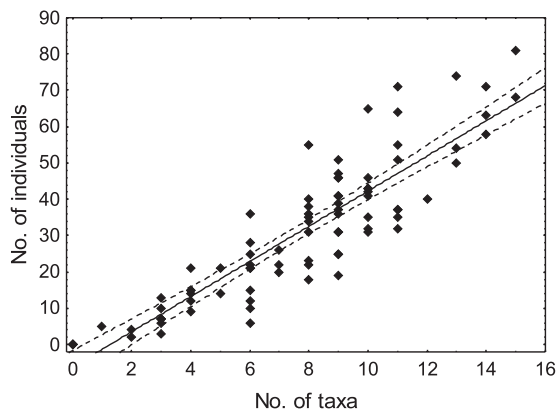
univariate significance levels. The arguable omissions are documented in Results. In the first two steps, the significance level was set at  $P < 0.15$  (to retain variables that could gain significance in combination with other variables); in the final step,  $P < 0.05$  was used. Performance of the final multivariate models was assessed by comparing observed vs. expected presence/absence using the breakpoint at 0.5 for the expected values.

We tested the effect of pond management by adding the fact of management to the final multivariate model of each species. In the crested newt model, we reclassified the original eight land-cover types to five types (forest, field, dry grassland, meadow and shrub/urban; i.e. neglecting the presence of forest in open areas) to avoid combinations with zero or single observations.

To compare niche breadths, we used the generalist-specialist metric ( $\theta$ ) derived from the beta diversity of amphibian communities (Fridley *et al.*, 2007). The use of  $\theta$  is based on the assumption that specialist species, on average, should co-occur with fewer species than generalists. In 100 simulations for each species, we randomly selected 20 sites of its occurrence and calculated beta diversity of the sub-sample by subtracting from the total amphibian species richness the average number of species per pond.

## RESULTS

Crested newts were found in 99 ponds (47%) and smooth newts in 136 ponds (65%) of 210. Among the 148 occupied ponds, 87 (59%) were inhabited by both species, 49 (33%) by



**Figure 2** Relationship (linear regression with its 95% confidence bands) between invertebrate abundance and diversity per 10 dip-net in 85 ponds ( $y = 4.8x - 6.1$ ; coefficient SE = 0.3;  $P < 0.001$ ;  $R^2 = 0.80$ ).

the smooth newt and 12 (8%) by the crested newt only. The smooth newt was more common and abundant (mean  $11.2 \pm 1.2$  SE of caught individuals per occupied pond) than the crested newt ( $7.3 \pm 0.7$  SE). However, local maximum numbers of the species were rather similar: 69 larval and 20 adult smooth newts per 10 dip-net catches, and 37 larvae and 50 adults of the crested newt.

Fish were recorded in 24 ponds, each pond occupied by one species: 16 ponds by nine-spined stickleback (*Pungitius pungitius*), six ponds by the crucian carp (*Carassius carassius*) and two ponds by common carp (*Cyprinus carpio*). Both newt species avoided ponds with fish – larvae of the smooth newt were found in six (25%) such ponds (four times with sticklebacks, twice with common carps), of which two (one with sticklebacks, another with the carp) were also inhabited by

the crested newts (8%). These occupancy levels did not differ between the newt species (chi-squared test:  $\chi^2_1 = 2.4$ ,  $P = 0.12$ ), but contrasted with the 70% occupancy ( $\chi^2_1 = 18.8$ ,  $P < 0.0001$ ) and 52% occupancy ( $\chi^2_1 = 10.3$ ,  $P = 0.0013$ ) of these species in the other ponds respectively. Fish presence was not a simple correlate of pond size: the ponds hosting fish encompassed 69–11,550 m<sup>2</sup> (median 660 m<sup>2</sup>), which did not differ significantly from the ponds without fish (median 413 m<sup>2</sup>; Wilcoxon Matched Pairs test:  $P = 0.1$ ).

In the final set of 140 ponds without fish, crested newt presence was explained by three characteristics (Table 3): land cover within 50 m, the invertebrate diversity in the pond and the distance to the nearest pond occupied by conspecifics (Fig. 3). Notably, combinations of open land and forest were always superior over a single land-cover type around the pond, and open lands were used in the sequence of their naturalness (dry grassland > meadow > field) (Table 4). Altogether, the multivariate model classified 74% of observations (86% presences, 59% absences) correctly. At the univariate stage, four other factors appeared significant ( $P \leq 0.05$ ; Table 1): (1) the width of the buffer zone (uncultivated land) around the pond (positive), which was largely redundant with the land cover within 50 m (see Table 2), but had much smaller explanatory power than the latter; (2) the cover of tall vegetation in the pond (negative), which lost its significance when added to three of the four more significant variables, including the correlated and biologically more meaningful measure of invertebrate diversity; (3) sediment type (sand preferred; Table 4), which lost even its marginal significance in any combination with the two remaining (and more significant) continuous variables; and (4) water colour (clear water preferred; Table 4), for which the only significant multivariate model (combination

**Table 2** Redundancy of the ecological variables, which attained  $P \leq 0.15$  for either species in univariate analyses. See Table 1 for acronyms and sample sizes.

Variable	Related variables <sup>a</sup>
Shallow	Buffer***, Water*, Land cover < 50 m**, Open***, Invert.*
Buffer	Slope***, Shallow***, Sediment***, Water***, Land cover < 50 m***, Open*, Near. T.c. pond***, Invert.*
Slope	Buffer***, Land cover < 50 m*
Sediment	Buffer***, Water***, Vege > 1 m**, Near T.c. pond*
Water	Shallow*, Buffer***, Sediment***, Invert.**, Near T.c. pond*
Land cover < 50 m	Shallow**, Buffer***, Slope*, Ponds < 100 m*, Open**, Invert.**, Near T.c. pond*
Ponds < 100 m	Land cover < 50 m*, Near T. v. pond***, Near T.c. pond*
Ponds 200–500 m	Vege > 1 m*, Near T. v. pond**, Open**
Near. T.v. pond	Ponds < 100 m***, Ponds 200–500 m**
Near. T.c. pond	Buffer***, Sediment*, Water*, Land cover < 50 m*, Ponds < 100 m*
Vege > 1 m	Sediment**, Ponds 200–500 m*, Floating*, Open***, Invert.**
Floating	Vege > 1 m*
Open	Shallow***, Buffer*, Land cover < 50 m**, Ponds 200–500 m**, Vege > 1 m***
Invert.	Water**, Shallow*, Buffer*, Land cover < 50 m**, Vege > 1 m**

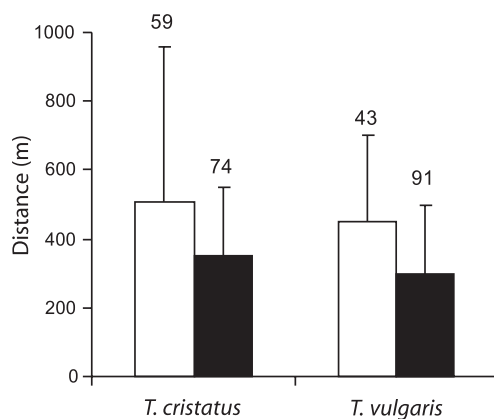
<sup>a</sup>Significance according to Spearman correlation (continuous variables), chi-squared test (categorical variables) or Kruskal–Wallis ANOVA (combination of the two): \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Table 3** Results of logistic regression models of habitat factors explaining the presence of the crested newt (*Triturus cristatus*) and the smooth newt (*Triturus vulgaris*) in 140 ponds<sup>a</sup>.

Variable	Estimate	SE	LL	$\chi^2$	P-value
<i>Triturus cristatus</i> (model log-likelihood -72.7, $P < 0.0001$ )					
Land cover < 50 m			-90.3	35.3	< 0.001
Near. T.c. pond	-0.21	0.14	-75.5	5.6	0.018
Invert.	0.11	0.05	-75.5	5.6	0.018
<i>Triturus vulgaris</i> (model log-likelihood -68.5, $P < 0.0001$ )					
Sediment			-66.3	16.4	< 0.001
Near. T.v. pond	-0.82	0.37	-80.5	4.2	0.040
Invert.	0.14	0.05	-74.5	12.0	< 0.001

<sup>a</sup>The between-group contrasts of categorical variables are indicated in Table 4; LL – log-likelihood of the variable.



**Figure 3** Median distances (with upper quartiles as whiskers) from the ponds occupied (black bars) or unoccupied (white bars) by the two species of newts to the nearest ponds occupied by their conspecifics. Note that for the independence of observations, no ponds closer to each other at 200 m was analysed; i.e. the values are systematically overestimated and no lower limits can be shown. The numbers are sample sizes.

with the distance to the nearest pond inhabited by conspecifics) performed much worse (log-likelihood 83.2,  $\chi^2 = 16.3$ ;  $P = 0.0027$ ) than the alternative selected by us (cf. Table 3).

Smooth newt presence was also explained by three characteristics (Table 3): the invertebrate diversity in the pond, sediment type (sand preferred; mud avoided; Table 4) and the distance to the nearest pond occupied by conspecifics (Fig. 3). The multivariate model classified 74% of observations correctly (88% presences, 44% absences). In the univariate stage, two other factors – overlapping with those in the crested newt – appeared significant ( $P \leq 0.05$ ): water transparency or colour (Table 4), and the cover of tall vegetation in the pond (negative). Again, vegetation cover was omitted because of its redundancy with the highly significant invertebrate diversity. Water colour co-varied with sediment type but performed less well in multivariate models: the only significant combina-

**Table 4** The occupancy of 140 ponds by the crested newt (*Triturus cristatus*) and the smooth newt (*Triturus vulgaris*) in relation to sediment type, water colour, land cover within 50 m and management status of the pond.

Variable	No. ponds	Pond occupancy (%) <sup>a</sup>	
		<i>Triturus cristatus</i>	<i>Triturus vulgaris</i>
Sediment		U	M
Clay	51	59	75**
Sand	16	81*	100**
Mud (mud layer > 40 cm)	63	52	60
Peat <sup>c</sup>	10	30	40
Water		U	U
Clear	84	67*	83**
Brown	18	44	56
Algae-green	6	50	50
Muddy <sup>c</sup>	32	38	41
Land cover < 50 m		M	U
Field (cultivated arable land)	26	15**	69
Field + forest	17	59	59
Dry grassland	15	74	80
Dry grassland + forest	13	92*	85
Meadow	19	58	58
Meadow + forest	23	74	83
Forest	15	60	60
Other (shrub + urban) <sup>c</sup>	12	42	50
Management		M	M
Unmanaged <sup>c</sup>	72	49	54
Restored/dug new	68	65	84*

<sup>a</sup>Significance of the difference from comparison group (<sup>c</sup>) according to univariate (<sup>U</sup>) or multivariate logistic regression model (<sup>M</sup>). \* $P < 0.05$ ; \*\* $P < 0.001$ .

tion (with invertebrate diversity – also redundant) was worse (log-likelihood 73.8,  $\chi^2 = 26.7$ ;  $P < 0.0001$ ) than our alternative (cf. Table 3). In contrast to the crested newt model, land-cover type within 50 m did not approach significance even in the univariate stage (Table 1).

Altogether, nine species of amphibians were recorded in the 140 ponds. Beta diversity of the amphibian communities did not differ between the ponds occupied by the newt species: the simulation-based  $\theta$  values per 20 ponds were  $4.2 \pm 0.9$  (SE) for the crested newt and  $4.4 \pm 0.8$  (SE) for the smooth newt.

Both species occurred significantly more often in managed (restored or dug anew) than in unmanaged ponds (Tables 1 & 4). In accordance with the model results, pond management effect for the crested newt was highly dependent on the surrounding land cover: 89% of the 19 managed ponds in the preferred dry grasslands or dry grassland-forest mosaics were occupied, compared to 56% of the 70 ponds in other habitats ( $\chi^2_1 = 8.5$ ;  $P = 0.004$ ). However, the management status contributed significantly to the multivariate model in the smooth newt only (log-likelihood = -73.1;  $\chi^2 = 6.0$ ;

$P = 0.014$ ); there was no such independent effect for the crested newt (log-likelihood =  $-72.6$ ;  $\chi^2 = 0.6$ ;  $P = 0.45$ ). Note that the distances from managed ponds to the nearest ponds inhabited by newts were taken into account in these multivariate analyses; the median distances being 350 m for the smooth newt (quartiles 250 and 520 m) and 390 m for the crested newt (quartiles 280 and 770 m).

## DISCUSSION

### Habitat-related explanations to population trends

The niche comparisons presented here considered only two related species in a small region and thus should not be over-generalized. However, such a restriction enabled us to avoid most methodological problems and alternative explanations when exploring the niche-related hypotheses of rarity (see Gaston *et al.*, 1997). Therefore, our study complements similar results obtained using more general methods in large heterogeneous communities (Gregory & Gaston, 2000; Heino, 2005).

Our results on the two newt species having contrasting conservation status do not support the niche-breadth (resource or habitat specialization) hypothesis of rarity (see also Gaston *et al.*, 1997; Gregory & Gaston, 2000; Marsden & Whiffin, 2003; Thompson & Ceriani, 2003; Walker, 2006), as judged from both the performance of the multivariate habitat models and the community analysis. The habitat modelling indicated that a similar number of variables explained to a similar extent the presence of the two species. At the scale studied, the models captured most of the variance in the species' presence, i.e. it is not likely that key variables for any species were missed. Rather, in terms of the fundamental niche (see Pulliam, 2000), both species may depend on the variables measured even more than observed, as indicated by the clearly lower classification success for absences. The latter, combined with the significant effect of adjacent source populations, suggests that several suitable sites were unoccupied as a result of stochastic extinctions and dispersal limitation. To a lesser extent (see Methods), the absence models may have contained random noise due to undetected presence, which for dip-netting is unlikely to co-vary with the habitat variables extracted (Gu & Swihart, 2004). Importantly, our variable set comprised a direct measure of food supply (diversity of invertebrates), which indeed appeared more significant for both species than its correlates (see Table 2). Given that the feeding niche partitioning may be even more important than the microhabitat partitioning for the coexistence of these generalist predators (Griffiths & Mylotte, 1987; van Buskirk, 2007), its inclusion as a part of the habitat (see Hall *et al.*, 1997) clearly improved the relevance of the models. The community-diversity method (Fridley *et al.*, 2007) is explicitly a hypothesis itself; however, we consider it an important attempt to operationalize the niche-breadth hypothesis, which otherwise may remain untestable (see Gaston *et al.*, 1997).

These results are unlikely to be significantly influenced by competitive exclusion or predation. First, such interactions between these species are strong in very small ponds only (van Buskirk, 2007), not of the sizes typical in the Danish landscapes and studied by us (see also, Griffiths & Mylotte, 1987; Dolmen, 1988). Second, for a significant competition impact to our analyses, one would expect many sites occupied by the larger species only. Actually, such sites formed 8% of newt occurrences, while the main difference in the spatial distribution of the species came from the ponds occupied by the smooth newt only. The absence of the larger species from so many ponds, in turn, was an unlikely result of insufficient quantity of resources (carrying capacity), because pond size had no influence on the incidence of either species.

Therefore, though additional impacts may exist, we suggest that the rarity and/or continuing decline of the crested newt, as well as the impression of its more pronounced specialization to the aquatic habitat than in the smooth newt (Cooke & Frazer, 1976), are related to particular habitat qualities – its niche position in relation to the currently prevailing conditions. Land cover around the pond was crucial: the most natural habitats (particularly a mixture of dry grassland and forest with > 90% of ponds inhabited there) were essential for the crested newt, while the surrounding habitat lacked any effects on the smooth newt. Differing abilities of the two species to use terrestrial habitats have been described by Müllner (2001) who found that crested newts leaving the pond usually oriented towards the forest, while smooth newts often stayed in the wet zone of the pond and 25% of the individuals migrated to open grasslands. Therefore, the declines of the crested newt in the North European Lowland could have lasted for centuries along with the replacement of natural forest-grassland mosaic with arable lands, and the further intensification of agriculture. Amphibian communities have also appeared to stabilize in stable, extensively managed agricultural landscapes (Crochet *et al.*, 2004). We suggest that these differing landscape-change effects on the two newt species are an example of a process that creates rare-common contrasts in related species pairs.

Potential threat factors related to the water-body characteristics were less clear and may apply to both species. Notably, pond sediment was important for the smooth newt but may have had some influence on the crested newt as well, for the occupancy on the sediment gradient varied similarly in both species (sand > clay > mud > peat; Table 4). In addition, there were univariate effects in two related variables – preferences for clear water and low cover of tall vegetation, which both correlated significantly with the sediment type (Table 2). All these are obviously related to water quality and chemistry, and suggest some sensitivity of both species to eutrophication. In ponds on peat or mud, the humic substances lead to lower transparency and/or brownish colour of the water, as well as to lower pH, and often low oxygen concentrations (Brönmark & Hansson, 2005). Vegetation taller than 1-m shades the pond, thus affecting negatively the larval development of newts (Oldham *et al.*, 2000; Sztatecsny *et al.*,

2004); such vegetation often indicates the influx of nutrients from households or fields as well.

### Pond management for rare amphibians

The support to niche-position hypothesis highlights the potential of habitat restoration for threatened amphibians in general, and for the crested newt in particular. For that, species-specific habitat requirements should be taken into account as a general pond management appears to support common species mostly (in our case: the smooth newt; see also Stumpel, 2004). For the crested newt, such habitat demands are a mosaic landscape of grassland and forest around suitable water bodies. Additionally, given that pond management sets its successional stage back, the weakness of a short-term effect to the crested newt may result from its preference for a more advanced succession stage (Sztatecsny *et al.*, 2004).

It was confirmed once again that fish presence is a major limiting factor for pond-breeding amphibians (Joly *et al.*, 2001; Brönmark & Hansson, 2005; Skei *et al.*, 2006). Fish can influence particularly the species having nektonic larvae, such as the crested newt (Joly *et al.*, 2001; Skei *et al.*, 2006). Therefore, introduction of fish to amphibian breeding ponds must be avoided.

Both newt species appeared to benefit from adjacent source populations (as suggested by Gill, 1978), confirming the key role of dispersal possibilities for amphibian management (Semlitsch, 2000). Dispersal limitation is also the key process that may produce both a low occupancy of sites and a low local abundance in relation to habitat availability (Venier & Fahrig, 1996). However, simple density of ponds did not predict the newt presence well, which may reflect a high, and varying, proportion of ponds unfavourable for settlement (Pope *et al.*, 2000) or survival. Though Joly *et al.* (2001) found a positive relationship between newt occurrence and the number of ponds within 50 ha surroundings, newly created ponds and ponds filled with alluvium were omitted in their study. Thus, knowledge about the distribution of successfully reproducing amphibian populations ('source' ponds) could greatly increase the efficiency of pond restoration.

### ACKNOWLEDGEMENTS

We thank L.C. Adrados, F. Bibelriether, N. Damm, I. Lepik, M. Linnamägi, P. Pappel, A. Päivärinta, P. Skriver and W. de Vries for help in the field. L.C. Adrados also created the database and entered the data. D. Green and three anonymous referees provided very constructive criticism on the manuscript. EU LIFE-Nature project LIFE04NAT/EE/000070, European Regional Development Fund (Centre of Excellence FIBIR), the Estonian Ministry of Education and Science (target-financing project 0180012s09) and the Estonian Science Foundation (grant 7402) provided financial support.

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Editor: David Green