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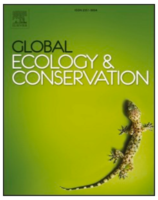

Decadal data reveal declines, not species replacement, of salamanders under agrarian reform

Jan W. Arntzen [1]

Institute of Biology, Leiden University, Leiden, The Netherlands, Naturalis Biodiversity Center, Leiden, the Netherlands

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ABSTRACT

Long-term data are uniquely suited to test hypotheses on processes in ecology, contemporary biogeography and conservation. I tested for species replacement among crested and marbled newts (genus *Triturus*) in western France, for which historical data showed a mutual range shift of 1 km per year. *Triturus* population sizes were estimated in 23 ponds from 1979 to the present. The data show a massive amphibian decline from pond infilling, succession and neglect, arising from the agrarian transition from cattle to arable farming. In eight persisting ponds, *Triturus* populations declined in unmanaged ponds and were stable in two managed ponds. Species composition was stable or changed in either direction. The absence of further notable species replacement is in line with population isolation by less dispersal from fewer and smaller populations in a thinning network of ponds. It is concluded that the large-scale agrarian reform that progressed over the post-World War II period intervened with, and eventually frustrated the original aim of the research project.

1. Introduction

Research projects are typically confined to a three-to-five-year time span, in line with granting systems. Ecologists are increasingly aware that these regular projects yield limited knowledge of temporal changes in population dynamics (Reinke et al., 2019) and ecological communities (Franklin, 1989, Magurran et al., 2010, Lindenmayer et al., 2012). More long-term studies are needed, because these are uniquely suited to follow changes in biodiversity through time, towards a better understanding of the dynamics of ecosystems, communities, and populations. The plea for long-term data gathering is equally justified for the fields of contemporary biogeography and conservation biology (e.g., Monsarrat et al., 2019, Kissel et al., 2025), because distributions and occurrences that appear steady in the short run may turn out to be in flux when studied for longer periods. In amphibians, outstanding examples of documented range shifts are the expansion of the invasive toad *Rhinella marina* over northeastern Australia (Eastal, 1981, Urban et al., 2008) and the shrinking range of the toad *Bombina variegata* over the west of France (Lescure et al., 2011). Upon inspection these examples also illustrate that expansions are easier to track than range regressions. However, the edge of one taxon's distribution often abuts that of another, closely related taxon (Darwin, 1859, Rapoport, 1982, Bull, 1991, Case and Taper, 2000). The advantages of two-species systems in the study of range border dynamics are that: i) the species are not necessarily rare, ii) analyses can be performed without difficult-to-justify absence data, and iii) shortcomings in data gathering such as uneven sampling plausibly apply to either species in equal terms (Arntzen, 2023ab). Conditions are that the species negatively affect one another (with competitive exclusion as

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E-mail address: pim.arntzen@gmail.com.

[1] ORCID – 0000–0003-3229–5993

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the ultimate outcome) and do not frequently hybridize (as not to form wide intergradations).

I set out to study species replacement among two competing and infrequently hybridizing salamander species, *Triturus cristatus* and *T. marmoratus* in an agricultural setting in the west of France. These 'large bodied newts' form a remarkable system for comparative research because their ranges overlap over ca. 150 thousand km^2 (28 %) of continental France, where they frequently share breeding ponds (Vallée, 1959, Schoorl and Zuiderwijk, 1981). Yet, both species are usually unequally frequent and this gives rise to an ecological mosaic in which the one or the other dominates. Environments with a preponderance of *T. cristatus* are mostly flat and open whereas *T. marmoratus* areas are hilly and forested (Schoorl and Zuiderwijk, 1981, Arntzen, 2023ab). The current study was designed to document the absolute and relative abundances of *T. cristatus* and *T. marmoratus* over time. The work was triggered by the observation that *T. cristatus* had been superseding *T. marmoratus* over the southern part of the département (dept.) Mayenne under agrarian reform (Vallée, 1959, Schoorl and Zuiderwijk, 1981, Arntzen and Wallis, 1991, Visser et al., 2017; see Table 1). To test if the documented *T. cristatus* – *T. marmoratus* species replacement in the post-World War II period was to carry through, a baseline data set was established of small and accessible water bodies, each with a substantial *Triturus* population. Populations were as much as possible followed into the current decade.

2. Materials and methods

Research was carried out in the northeastern part of dept. Mayenne in the west of France. Based upon an initial survey in 1979 (Schoorl and Zuiderwijk, 1981), 23 ponds were selected for long-term monitoring (Fig. 1). The main selection criteria were small pond size, high population density and good accessibility, with a preference for *T. marmoratus* dominated ponds because this was the species perceived to be losing out in competition with *T. cristatus*. All sites were field ponds intended for cattle water supply, except for two abandoned sand quarries. Brief pond descriptions are presented in Table 2.

Captures were made in spring or early summer with the dipnet (42 surveys), with funnel traps (eight times), by using a barrier and pitfalls (one time), by torching (four times), or by a combination of methods (four times). Animal marking was done by batch-mark toe clipping. In some surveys, individuals were individually identified by toe-clipping (Woodbury, 1956), from their ventral (*T. cristatus*) or dorso-lateral coloration pattern (*T. marmoratus*) (Hagström, 1979, Arntzen et al., 2004) or using PIT-tags (Faber, 2001). For batch-mark data sets estimates of the adult *Triturus* population size ($\widehat{N}$) were made by capture-mark-recapture analysis developed by Schnabel (1938) and Schumacher and Eschmeyer (1943) and that are implemented in the software FishMethods (Nelson and Nelson, 2023). Methods were chosen between on account of the precision they provided (i.e., narrow 95 % confidence intervals). For surveys with individually recognized newts the 'closed captures under full likelihood p and c' was used in software MARK (White and Cooch, 2001, White, 2008, Cooch and White, 2008). Capturing with funnel traps is not only practical and efficient (Arntzen and Zuiderwijk, 2020; Arntzen, 2025), but in principle also fits the assumption of equal sampling effort from one sampling session to the other. Such data were analysed with the 'Removal' routine as implemented in the software FSA (Ogle, 2016) under default settings. This method is based on the depletion of the number of unmarked animals in the population and 'removal' is not to be taken literally. Finally, two population size estimates were derived from genetic profiles observed in the offspring (Jehle et al., 2005). The two species occasionally hybridize to give rise to a morphologically distinct class of adult F_1 hybrids (Vallée, 1959, Arntzen et al., 2021, Arntzen, 2024). Hybrids were taken to indicate the presence of both species. Juveniles were occasionally observed for *T. cristatus*. These were either ignored or subjected to an independent population size estimate.

3. Results

Fifteen ponds (65 %) disappeared over the 1979–2025 period, mostly due to infilling, succession, and neglect (Figs. 1 and 2, Table 2). Land use around these localities remained pasture (three times) or changed from pasture to arable (12 times). Of the eight persisting ponds (35 %) three lost their original field aspect due to encroaching forestation from lack of maintenance (pond 2F8), for hunting purposes (158 and 2A1) and one became stocked with fish (136). These four ponds had small populations in 2024, as determined from small numbers of *Triturus* eggs in spring (JWA and R. Jehle, personal communication). Adult population sizes fluctuated, with pond 222 as an extreme example ($33 \leq \widehat{N} \leq 535$; Fig. 3). In other ponds with four or more annual estimates over three or more decades the total adult population size went down by an order of magnitude in pond 2A1 ($15 \leq \widehat{N} \leq 205$), was stable in pond 232 ($163 \leq \widehat{N} \leq 217$), or was stable and then decreased in 278 ($19 \leq \widehat{N} \leq 220$) and 2D5 ($24 \leq \widehat{N} \leq 185$). Unchallenged *Triturus* populations are only found in two ponds that are actively maintained (ponds 222 and 232). For details see Supplementary Material.

Table 1
Summary of results for three surveys on the distribution of *Triturus* species over dept. Mayenne in the west of France at ca. three-decade intervals. Note that the frequency of syntopic populations did not change much in the period following World War II, despite a marked overall shift from *T. marmoratus* to *T. cristatus*.

Period	Number of ponds			Data source
	T. cristatus	*T. marmoratus*	Both species #	
1945–1955	25 (24.0 %)	54 (51.9 %)	25 (24.0 %)	Vallée (1959)
1979–1980	73 (47.4 %)	37 (24.0 %)	44 (28.6 %)	Schoorl and Zuiderwijk (1981)
2014–2015	50 (49.0 %)	29 (28.4 %)	23 (22.5 %)	Visser et al. (2017)

Hybrids are taken to represent both species

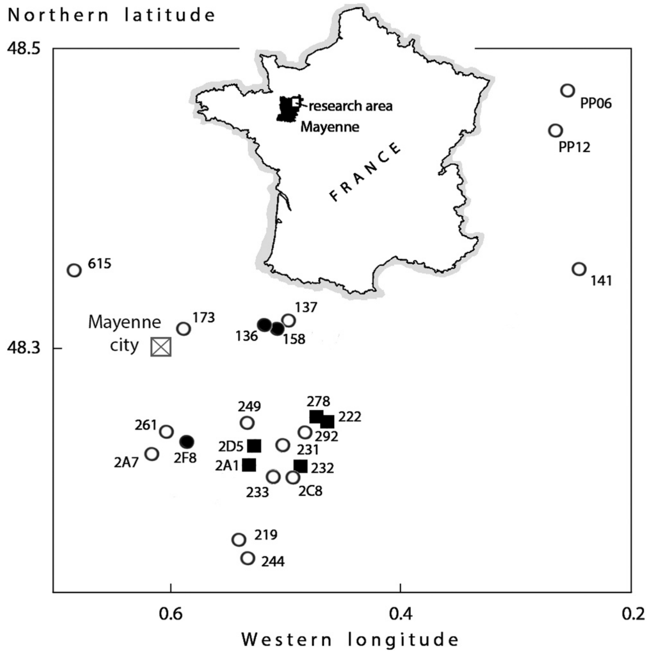

Fig. 1. Position of 23 research localities in the northeast of dept. Mayenne in the west of France. Open round symbols represent the 15 ponds that disappeared over time. Solid symbols represent persisting ponds, five of which shown by square symbols were followed for *Triturus* population size development.

Table 2
Brief description of characteristics and fate of 23 ponds selected for the study of *Triturus cristatus* and *T. marmoratus* population size development and species replacement in dept. Mayenne, France, from 1979 to the present. See also Fig. 1.

Pond number	Pond characteristics and fate	Principle land use in 2024
136	Medium sized field pond in pasture at forest edge. Fish introduced after 2012 and pond too large for manual removal. Persisting at low population size as judged from egg-deposition in spring 2024.	Pasture
137	Small field pond in pasture. Filled in.	Arable
141	Small field pond in pasture. Filled in.	Arable
158	Medium sized field pond in pasture. Persisting, but turned into a deeply shaded forest pond with a small population as judged from egg-deposition in spring 2024.	Forest
173	Sand quarry with pond of fluctuating size. Filled in.	Arable
219	Small field pond in pasture. Gradually disappearing through succession, by now gone.	Pasture
222	Sand quarry with pond of fluctuating size. Persisting, actively maintained. Introduced fish removed manually in 1988. Population size and species composition followed over the decades.	Sand quarry
231	Small field pond in pasture. Filled in.	Arable
232	Medium sized field pond in pasture. Persisting, actively maintained. Population size and species composition followed over the decades.	Garden
233	Small field pond in pasture. Filled in.	Abandoned pasture
244	Medium sized field pond in a domestic setting. Filled in. New large pond created nearby later.	Arable
249	Small field pond in pasture. Filled in.	Arable
261	Medium sized field pond in pasture. Disappeared over time for lack of maintenance, with mechanical cattle drinking facility now in use.	Pasture
278	Small field pond in pasture. Persisting spring pond but reduced in size. Population size and species composition followed over the decades.	Pasture
292	Small field pond in pasture. In 1984 introduced fish manually removed. Filled in.	Arable
615	Small field pond in pasture. Filled in.	Arable
2A1	Small field pond in pasture. Persisting, but turned from open field pond for cattle drinking to entirely shaded. Population size and species composition followed over the decades.	Forest
2A7	Small cattle drinking facility in a farmhouse setting. Disappeared over time for lack of maintenance.	Arable
2C8	Shallow field pond that gradually disappeared through succession, by now completely gone.	Arable
2D5	Small field pond in pasture at forest edge. Persisting but reduced in size and increasingly shaded. Population size and species composition followed over the decades.	Pasture
2F8	Small field pond in pasture. Persisting, but turned from open field for the watering of cattle to shaded pond with a marginal population as judged from egg-deposition in spring 2024.	Arable
PP06	Small field pond in pasture. Filled in.	Arable
PP12	Small field pond in pasture. Filled in.	Arable

Fig. 2. Example of a *Triturus* breeding pond that disappeared from agrarian reform, with land use changing from cattle grazing in 1981 (top image) to arable in 2024 (bottom image).

Five ponds had single-species populations of *T. cristatus* (pond 244) or *T. marmoratus* (141, 173, 615 and PP06). Ponds with both species were dominated by *T. cristatus* ($F_c>0.8$, 33 % of observations), by *T. marmoratus* ($F_c<0.2$, 37 % of observations) or by both species at about even ($0.2 <F_c<0.8$, 29 % of observations). In syntopic populations, species composition for the first versus the last year of study showed significant shifts in favour of *T. cristatus* in two ponds (Fisher's exact test, $P < 0.05$ in pond 136 and $P < 0.0001$ in pond 232), in favour of *T. marmoratus* in two ponds ($P < 0.001$ in pond 222 and $P < 0.0001$ in pond 249) and no significant change ($P > 0.05$) in another seven ponds ($P > 0.05$ in 158, 233, 278, 292, 2A1, 2C8 and 2D5). Numbers of *T. cristatus* juveniles were small except for pond 244 in 1979 when the cohort size ($\widehat{N}=562$) was substantial relative to the adult population size ($\widehat{N}=951$). The frequency of *T. cristatus* x *T. marmoratus* F_1 hybrids across 18 syntopic populations was 2.6 % (range 0–26 %).

4. Discussion

Obtaining long-term data may be a promising avenue for gaining insights into ecological and population dynamic processes (Franklin, 1989, Reinke et al., 2019), but is easier said than done (e.g., Lindenmayer, 2018). The present project on the contemporary biogeography of competing newt species started late last century with a wide variety of ponds and populations. It was initiated to gain insight into pattern and process of the expansion of *T. cristatus* at the expense of *T. marmoratus* that was anticipated from two department-wide surveys following World War II, with a three-decade interval (Vallée, 1959, Schoorl and Zuiderwijk, 1981). Alternatively, insight in the species' shifting ranges were obtained from distribution models for *T. cristatus* and *T. marmoratus*, either considered jointly (Arntzen, 1996, 2023ab) or separately (Préau et al., 2018, 2020, 2022).

The overriding result is that *Triturus*-populations have drastically declined through the removal of breeding localities and lack of pond maintenance. Although the study ponds were chosen on account of *Triturus* species, other indigenous amphibian species known for western France were encountered before the year 2000 and declined similarly (species not observed were the frog *Pelodytes punctatus* that is locally restricted to ephemeral habitats and *Bombina variegata* that may have disappeared from the department altogether (Baudin, 2010, Lescure et al., 2011)). It may be assumed that the decline in pond numbers and pond quality was detrimental to other organisms also, such as aquatic invertebrates (Davies et al., 2008, Hassall, Hollinshead and Hull, 2012, Biggs and Williams, 2024).

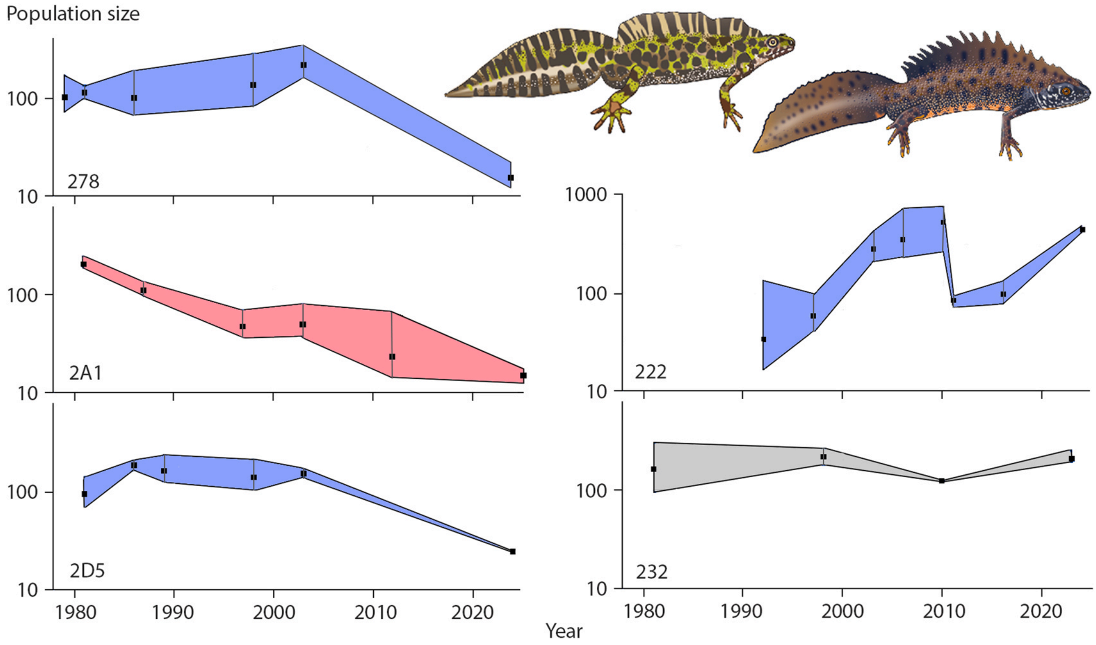

Fig. 3. Development of *Triturus* populations in five ponds with four or more population size estimates ($\widehat{N}$, solid squares) over three or more decades. The shaded surfaces encompass the 95 % confidence intervals of the estimate, with a *T. cristatus* dominated pond in red, three *T. marmoratus* dominated ponds in blue and a pond with both species frequent ($0.8 < F_c < 0.2$) in grey. The three ponds to the left are not maintained and gradually lost their potential as *Triturus* breeding sites from succession (pond 278), encroaching forestation (2A1), or both (2D5). Species composition changed significantly in favour of *T. marmoratus* in pond 222 and in favour of *T. cristatus* in pond 232 (for details see text and Supplementary Material). Animal drawings are *T. marmoratus* (left) and *T. cristatus* (right) by Bas Blankevoort, Naturalis Biodiversity Center.

Cattle grazing is in decline so that cattle watering places become obsolete. The policy underlying this trend is the switch to conserved forage for indoor farming. The process is accompanied by hedgerow removal and land use conversion from pasture to arable, mostly to produce fodder corn, therewith aggravating pond loss (Figs. 3 and 4). It may be noted that the severity of pond loss is at par with other estimates for the dept. Mayenne (Table 3) and faster than in the United Kingdom (Wood, Greenwood and Agnew, 2003) and northwestern France (Curado et al., 2011). *Triturus* populations were also threatened by the introduction of fish, but in two instances these could be removed by intensive dip-netting in late summer. Access to ponds was sometimes problematic upon new ownership, but no surveys were stopped for that reason. Crucially, the good news is that ponds that were actively maintained (two out of 23) kept healthy and large populations and that enigmatic declines or losses were not observed. Population sizes fluctuated as is typical for amphibians (Marsh, 2001, Green, 2003) including *Triturus* newts (Arntzen and Teunis, 1993, Griffiths et al., 2010, Von

Fig. 4. Example of the post-World War II disappearance of the bocage landscape in the south of dept. Mayenne. Lines are hedgerows, stippled areas are orchards and shading is forestation, with from left to right the situation in 1949, 1977, 1992 and 2013 (from Arntzen, 1998, Visser et al., 2017). The situation around farmhouse 'les Féages' (F) is exceptional because, while hedgerows remained, pasture land with cattle grazing was eventually abandoned in favour of forestation for hunting practices.

Table 3

Loss of ponds and *Triturus* populations in dept. Mayenne, France over the post-World War II period, based upon the department-wide surveys by Vallée (1959), Schoorl and Zuiderwijk (1981), Visser et al. (2017) as well as the present study and JWA (present paper and unpublished data).

Study area	Entire department		Pre-en-Pail area	Present study
Period	~1950–1980	1979–2015	1997–2015	1979–2024
Temporal window (years)	~29	36	18	~40
Initial number of localities	104	145	46	23
Remaining	54	42	43	8
Idem, Triturus present	19	20	7	8 ($ 4)
Annual loss (percent)	5.7	5.4	9.9	2.6 ($ 4.3)
Population half-time (years)	12	12	7	26 ($ 16)

$ Considering four ponds with relict *Triturus* populations that turned low quality as lost

Bülow and Kupfer, 2019, Cayuela et al., 2020) and this involved the relative increase of one species over the other, but gains and losses were reported for both species. Several populations turned very small but none went extinct for stochastic population dynamic processes. The extensive, ca. 30 km wide species replacement documented for the post-World War II period (Arntzen and Wallis, 1991) did not carry on over the decades to follow as was also found in a third department-wide inventory (Visser et al., 2017; see Table 1 and discussion below).

It may be wondered if the choice for large initial populations in small ponds affected the outcome (Mentges et al., 2021). Obviously, large populations are more likely to get smaller than to get even larger and small ponds are probably more susceptible to succession and disappearance than bigger ones. It has been observed that *T. marmoratus* inhabits smaller ponds than *T. cristatus* (Schoorl and Zuiderwijk, 1981), but because the current study focusses on syntopic populations, it is unlikely that the bias worked out differently for the species. Besides, the use of funnel traps instead of the dipnet allows for the study of larger ponds and smaller populations (Arntzen and Zuiderwijk, 2020; Arntzen, 2025) but traps were not available when the project started. It has also been found that *T. cristatus* thrives in areas of higher pond density than *T. marmoratus* (Visser et al., 2017). The thinning of the pond network may therefore be more detrimental to that species than to *T. marmoratus* but this is not supported by the results. Forty years is seen as a typical age for pond renovation (Swartz and Miller, 2019) but the small ponds here considered require more regular maintenance to which de-shading, the removal of sediment and mitigating nutrient pollution are essential components, including the manual removal of duckweed (Sayer et al., 2012, López-de Sancha et al., 2025). While individual ponds need attention, it is the network of ponds that keeps the entire spatially structured population afloat (Fortuna et al., 2006, Hill et al., 2017, Horváth et al., 2019, Falaschi et al., 2020). A recent pond restoration project dealt with a small number of ponds (see Bouteloup, 2017). New ponds are also being created, but often these are garden ponds stocked with fish and wildfowl, with amphibians rare or absent.

Many factors are known to impact amphibian wildlife, including contaminants, UV-B irradiation, emerging diseases, the introduction of alien species and climate change (Beebee and Griffiths, 2005, Collins and Crump, 2009). Effects may be direct but could also affect the balance between interacting species, such as *T. cristatus* and *T. marmoratus*. However, the main parameter driving change in this system has been identified as agrarian reform, in particular field size enlargements and the removal of hedgerows with a negative impact on the more terrestrially operating *T. marmoratus* (Arntzen, 2024b) that subsequently loses out against the more aquatic *T. cristatus* (Arntzen, 2023a). Why did the scenario of further species replacement not unfold locally while hedgerow removal has been ongoing ? Three possible explanations are:

i) The species' mutual distribution had by 1980 stabilized against an environmental gradient encompassing more than just hedgerows, and species replacement should not have been expected. However, ecogeographical analyses over the entire area of species' range overlap suggest that even hilly and forested areas with *T. marmoratus* strongholds are eventually taken over by *T. cristatus* (Arntzen, 2023b).

ii) Species replacement proceeds at a pace too slow to be documented directly. This raises the question of why in the post-World War II period range changes were fast and substantial (Table 1, see also Visser et al., 2017: Figs. 1 and 2). The simple answer is that hedgerow removal was profound those days in the flat, southern part of the department where species replacement took place (Fig. 4; Arntzen and Wallis, 1991). A temporary increase in the interaction between the species from habitat disturbance is supported by the frequency of adult hybrids in syntopic populations at 19 % early on (Vallée, 1959) versus 2–7 % ever since (Schoorl and Zuiderwijk, 1981 and personal communication, Jehle et al., 2005, Arntzen and Hedlund, 1990, Arntzen et al., 2009, 2021, Arntzen, 2024ab, present study). A state of flux is, however, not supported by the balance of allotopic and syntopic populations that was stable at a ratio of ca. 3–1 (Table 1).

iii) The process of species replacement stalled due to lack of dispersal. Dispersal, which is the successful reproduction in a place different from where born, foremost depends on the number of emigrants of a population and their survival when on the move. If the number of breeding populations goes down and populations get smaller, the number of emigrants shrinks. Also in play are inter-pond distances and the quality of the intervening habitat (Halley et al., 1996, Marsh and Trenham, 2001). Assessing the 'compromised dispersal' explanation requires knowledge on the species' recruitment potential and metapopulation spatial organization.

Recruitment to the adult population was highly erratic in *T. cristatus*, with one observation of a large juvenile cohort (pond 244 in 1979) that accounted for 84 % of all juveniles observed (Supplementary Material). For *T. marmoratus* recruitment is enigmatic because juveniles are terrestrial and escape detection. However, the fluctuating *T. marmoratus* population size in pond 222, along with observations on large larval cohorts in 1981 and 2024 (JWA, unpublished data) suggests that recruitment is boom and bust for this species as well, so that juvenile dispersal is difficult to assess.

Pond loss hampers connectivity and without 'stepping stones' new areas cannot be colonized. In dept. Mayenne, *Triturus* populations increasingly persist in isolation with increased risks for extinction, but they are also less prone to a continued invasion by the competitive congener. The three explanations discussed are not mutually exclusive and none of them can currently be dismissed. The quantitative data of the experiment demonstrate a dramatic recent decline of both *Triturus* species, but this was not the purpose of the study (see also Krebs, 1991).

5. Conclusion

In view of testing the *Triturus cristatus* – *T. marmoratus* replacement hypothesis with long-term data, agrarian reform proceeded at an unanticipated intensity, intervened with, and eventually frustrated the research project. The land use practices involved are reallotments and hedgerow removal followed by the change from cattle to arable farming, inducing pond loss. The agrarian reform intervened with, and eventually frustrated the research project. At hindsight, equally informative results might have been obtained at a lower workload by arranging a subset of localities under the investigator's control. However, with one exception, agreement with property owners for long-term research and for pond maintenance could not be reached, whereas the acquisition of sites through a research grant, however affordable, would probably have been frowned upon.

Ethical approval

Fieldwork was carried out in accordance with international and local guidelines once these became implemented

Declaration of Competing Interest

None

Acknowledgement

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Open research statement

Results underlying this paper are presented in Supplementary Material

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03567.

Data availability

Results underlying this paper are presented in the Supplementary Material

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