Quantifying rarity of intraspecific diversity at multiple spatial scales by combining fine-grain citizen-based data across national boundaries

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ABSTRACT

Quantifying rarity at the intraspecific level is an important task for conservation biologists because rare phenotypes have a higher extinction risk than common ones. However, quantitative assessments of rarity are lacking at this level, preventing to adequately protect rare and endangered variants that are part of the pool of common species. Our aim was to take benefit of high-resolution volunteer-based occurrence data to assess quantitatively rarity patterns of facultative paedomorphosis, in the Alpine newt (*Ichthyosaura alpestris*). This polyphenism is composed of two morphs, a rare adult phenotype retaining gills and a common phenotype metamorphosing. We included multiple spatial scales (i.e., resolution) and combined 15,613 occurrence records from the atlas databases of the seven countries in the European Alps to understand how spatial scale may affect rarity metrics. Our analyses revealed that the rarer

phenotype was 292 times rarer than the common phenotype, occupying a very small and fragmented area of occupancy. Yet, rarity depended on the spatial resolution of the data. Rarity estimates were up to 1,300 times lower at the coarser than at the finer spatial scale. Both the rarity of the rare phenotype and the presence of threats (i.e., fish introductions) make paedomorphs critically endangered whereas the common phenotype was widespread at all spatial scales. Altogether, these results show how rarity metrics can differ between spatial scales for rare and common organisms, suggesting that fine-grain data should be used to assess intraspecific rarity. They also show that combining datasets from distribution atlases is efficient to estimate rarity.

1. Introduction

Intraspecific variation is a major, but often neglected component of biodiversity (Paz-Vinas et al., 2018; Reydon, 2019; Zhao et al., 2019; Des Roches et al., 2021). In many species, variation is exemplified by subspecies or lineages (Ryder, 1986; Fraser and Bernatchez, 2001; Haig et al., 2006), some of those being in fact sometimes cryptic species (Bickford et al., 2007; Yan et al., 2018). Intraspecific diversity can also take the form of polymorphisms in which alternative distinct phenotypes (i.e., morphs) coexist within a single species in organisms as different as invertebrates, fish, amphibians, birds and mammals (West-Eberhard, 2003; Lackey et al., 2019; Foster et al., 2021; Klann et al., 2021). The differentiation can involve some specific traits but also the whole development of organisms, their life cycle and habitat (Laudet, 2011; McNamara, 2012; Mulder et al., 2022). This is the case in several families of newts and salamanders expressing facultative paedomorphosis (Gould, 1977). In species with facultative paedomorphosis, a fraction of individuals in populations undergoes a full metamorphosis associated with shift from an aquatic to a biphasic life style, whereas another fraction skips metamorphosing and acquires sexual maturity at a larval somatic stage, remaining fully aquatic (Denoël et al., 2005b; Bonett et al., 2022; Fig. 1).

Regardless of the origin of intraspecific variation (e.g. genetic polymorphisms or polyphenisms), genotypes or phenotypes can have peculiar distribution patterns as a result of their adaptation to specific environments and their evolutionary history (Bush and Adams, 2007; Emel and Bonett, 2011; Thomasen et al., 2011; McLean and Stuart-Fox, 2014; Bonett et al., 2018; Oromi et al., 2018; Foster et al., 2021). This means that some variants may have an inherently smaller distribution range and be rarer than the species to which they belong, such as shown for facultatively paedomorphic newts (Denoël et al., 2001; Denoël, 2007), viviparous fire salamanders (Lourenço et al., 2019) and ovoviparous common lizards (Horreo et al., 2018). Being rarer may therefore mean that the less common variants could suffer a higher risk of extinction than the common variants. This is supported by anthropogenic environmental change causing new selective forces that may put at a disadvantage some alternative phenotypes such as in insect winged morphs following deforestation (Foster et al., 2021), anadromous fish

morphs after dam construction (Morita et al., 2009) or in paedomorphic newts following fish introductions (Denoël et al., 2009). In such cases, the species can survive but with an erosion or distribution change of its intraspecific diversity (Denoël et al., 2019b). At a broader extent, environmental changes are thought to have given rise to speciation with fixation of some morphs with now risks of extinction at the species level such as in the axolotl and the giant salamanders due to the acceleration of environmental degradation (Zambrano et al., 2007; Voss et al., 2015; Yan et al., 2018). However, as it stands, quantification of the relative rarity of the common and rare components of intraspecific diversity is so far unknown and this particularly over broad geographic areas. This results mainly from the fact that scientific research typically takes place where the variants of interest occur, then underestimating their rarity on broad geographic extents. This is particularly problematic because some species are common and do not benefit from conservation priorities whereas parts of their intraspecific biodiversity may be threatened at an unknown level (Degner et al., 2007; Taylor et al., 2020).

Research at the inter-specific levels can give us insights to depict rarity patterns of intraspecific diversity. First, several metrics of rarity have been proposed at the species level; that means to differentiate between common and rare species (Margules and Usher, 1981; Gaston, 1994). Relative appreciations of rarity among related species yield particular insights into where more attention needs to be paid (Blackburn and Gaston, 1997). Second, rarity estimates can be quantified at different spatial scales (Margules and Usher, 1981) and thus provide insights for improving our understanding of ongoing patterns and processes associated with rarity and for prioritizing conservation measures. Using appropriate spatial resolution is a prerequisite for evaluating rarity (Thomas and Abery, 1995; Hartley and Kunin, 2003; Joseph and Possingham, 2008; Keith et al., 2018). While species occurrence data is often very precise and detailed in local, regional or national atlases, they are yet often difficult to obtain for large geographic areas (Sillero et al., 2014). Albeit not published at the finest spatial resolutions, the original fine-grain records data are available in the databases of atlas and other biological records centers. Therefore, they represent an opportunity for multi-scale analyses of distribution patterns over large biogeographical regions (Sillero et al., 2018). The existence of such resource could prove particularly valuable to further understand how spatial scale could affect estimates of rarity of intraspecific diversity. This is essential as failing to use a correct spatial scale for rare phenotypes may lead to inadequate assessment and therefore conservation.

Our aim was to prone the use of rarity metrics at the intraspecific level and at multiple spatial scales by using citizen-based data to quantitatively highlight the relative risk of intraspecific biodiversity loss and how spatial scale could affect our ability to detect risk. By spatial scales, we mean here spatial resolutions, which are associated to different grain sizes; grain size being defined as the size of the elementary sampling units: Dungan et al., 2002; Legendre and Legendre, 2012. We studied, as a model system, facultative paedomorphosis in the Alpine newt (*Ichthyosaura alpestris*; Fig. 1) across an entire biogeographic region, the European Alps. We chose this species because it is not considered as being threatened with extinction by IUCN at the species level (IUCN SSC Amphibian Specialist Group, 2022), and therefore often not considered as a target in conservation plans whereas its populations of paedomorphs are believed to be rare and have suffered major declines (Denoël et al., 2001, 2005a, 2019). Specifically, we aim to show the usefulness of integrating and combining, at a

high resolution, multiple fine-scale citizen data accumulated in databases throughout the entire Alpine territory with researcher data at the intraspecific level. This offers therefore the possibility of testing the effects of spatial scale (i.e., resolution) in the assessment of intraspecific patterns of rarity and to further compare areas of occupancy (AOO) and extent of occurrence (EOO) at multiple spatial scales and in the two phenotypes.

Our main hypothesis is that a common species may be composed of rare phenotypes that deserve conservation priorities and that the use of coarse spatial scales may hide our perception of rarity levels of rare phenotypes. Specifically, we expect that the rare phenotype could be of several orders of magnitude rarer than the common phenotype but that only analyses using a small grain size (i.e., such as 1 or 4 km^2 rather than 100 km^2 or more particularly coarser grid cells) can prove valuable to infer their extreme rarity and therefore their conservation needs. Due to declines reported in previous studies and the general consideration of rarity of paedomorphosis, we also hypothesize that the rarity of paedomorphosis could be detected at multiple spatial scales, therefore also informing on the widespread pattern of extinction risk.

2. Methods

2.1. Delineation of the study area

We focused on the European Alps as defined by the Alpine Convention, the world's first international treaty considering a transnational mountain area in its geographical entirety with the aim of safeguarding sensitive Alpine ecosystems (Gerbaux and Zuanon, 1995; Kohler et al., 2008). The Alps cover a surface area of 190,726 km² and include parts of Austria, France, Germany, Italy, Slovenia, Switzerland, and all of Liechtenstein (Fig 2; Table A1).

2.2. Rare phenotype data

We combined our own field-based data on the occurrence of paedomorphic Alpine newts across the Alps acquired over the last 25 years with those available in the literature (Breuil, 1986; Denoël et al., 2001; Morand and Bovero, 2013; Deso and Roinard, 2015; Denoël et al., 2016; Heiss, 2017 and references herein) and inquiries from local specialists to depict their distribution (Table A2). Only strictly adult phenotypes (i.e., those expressing sexual traits such as a developed cloaca) were considered in this study (Denoël, 2017). This polymorphism has attracted much interest, and local populations of paedomorphs have been well described across their distribution range (see e.g. Denoël et al., 2001 and references herein). In contrast to local populations of metamorphs, which can be structured in networks of nearby ponds, typically within a distance of a few hundred meters (Cayuela et al., 2020), paedomorphs cannot disperse – except at a few meters of distance (Denoël, 2003) – from their water bodies. Because fish have been recognized as the main threat to the populations of paedomorphs (see e.g. Denoël et al., 2019b), we retrieved data on the presence of fish in the sites where paedomorphs have been found (Table A2).

Fig. 1. Intraspecific variation in the Alpine newt (facultative paedomorphosis): (a) the paedomorph, a rare phenotype retaining gills at the adult stage and (b) the metamorph, a common phenotype losing gills at metamorphosis. The figures depict males from the Alpes de Haute Provence, France (Photographs: Mathieu Denoël).

2.3. Citizen-based atlas data

We combined national and regional databases including citizen science and research-based data sets on the Alpine newt covering the entire extent of the study area. The data set includes altogether 15,613 observations (i.e., data points on the presence of local Alpine newt populations) accumulated by volunteers and researchers within the limits of the Alpine Convention (Fig. 2; Table A1). The distribution data include both new unpublished records and data published independently in the form of atlas at regional and national scales (i.e., not at a high resolution) using grid maps (Cabela et al., 2001; Sindaco et al., 2006; Meyer et al., 2009;

GHRA - LPO Rhône-Alpes, 2015; Andrä et al., 2019) or as points on maps, in the cases of Liechtenstein (Kühnis, 2002, 2011) and Bavaria (Andrä et al., 2019) with the exact locations kept confidential in all cases.

2.4. Mapping at multiple spatial scales

We used the European Environmental Agency (EEA) grids, which are a European standard particularly suitable for distribution analyses in the Alps because the grid cells have the same dimensions across the study area. Specifically, we used EEA grid cells at 1 x 1 km and 10 x 10 km, and from these, we created additional grid cells at 2 x 2, 5 x 5, 20 x 20 and 50 x 50 km to obtain different spatial scales (i.e., spatial resolutions using therefore grain sizes from high resolution: 1 km² to low resolution: 2,500 km²). We chose to use these spatial resolutions because 1 km² is the closest to the area used by a local population of the Alpine newt (Cayuela et al., 2020), 4 km² is typically recommended by the IUCN Red List to characterize areas of occupancy across taxa (IUCN, 2019); 25 km² and 100 km² fit regional and national distribution atlases, such as in Switzerland and Italy, respectively (Meyer et al., 2009; Sindaco et al., 2006); 400 km² corresponds to transnational cartographies, such as those previously done on the Alps (Gugerli et al., 2008), and 2,500 km² corresponds to continental atlases, such as the one produced for mapping European amphibians and reptiles (Sillero et al., 2014). We presented the maps only at spatial resolutions of 100 km² and above for conservation purposes and due to the database owners' confidentiality rules. We constructed the maps' relief background of maps using digital terrain elevation models and the delineation of countries by shapefiles, all provided open source by the EEA. Mapping was processed in QGIS 2.0 and ArcMap 10.5.

We projected the coordinates of metamorphic and paedomorphic Alpine newt sites (i.e., the exact position at the highest resolution available; Table A1) to the EEA grid system at the finest scale available throughout the studied area (1 km² grid cells). As some of the occupied cells were shared between neighboring countries, we removed duplicates for the calculation of the number of occupied cells.

2.5. Analyses

To analyse the effect of spatial scale on determining intraspecific rarity, we proceeded from the finest (1 km²) to the coarsest spatial grain available (2,500 km²). At all the spatial scales, we counted the number of grid cells with the known presence of metamorphic and paedomorphic Alpine newts. From the counts of occupied grid cells, we calculated two metrics for the two phenotypes: the area of occupancy (in km²) based on the number of occupied grid cells and the number of 1 km² grid cells used in each larger grid cell (i.e., from the 4 km² grid cells to the 2,500 km² grid cells (for a similar application in a study on birds, see e.g., Carrascal and Seoane, 2009)). To show the relative rarity of the rarest phenotype (the paedomorph) in comparison to the most common phenotype (the metamorph) across spatial scales, we also computed a third metric based on the area of occupancy. It was computed by dividing the area

of occupancy of the metamorphs by that one of the paedomorphs at each spatial resolution. Finally, we calculated the extent of occurrence (EOO) of the paedomorphs and metamorphs in the Alps using a minimum convex polygon. We further compared EOO to AOO at each spatial resolution from 1 km² to 2,500 km². We also identified threat occurrence (i.e., alien fish introduction) for the rarest morph for which this data is available.

We used linear models to test the fixed effects of phenotype and spatial scale (i.e., resolution from fine to coarse grain grid cells) on the area of occupancy (normal distribution) and the number of used grid cells (Poisson distribution) and to test the fixed effect of spatial scale on the relative index of rarity of paedomorphs on metamorphs (normal distribution). We used a log10 transformation of each variable to meet normality assumptions.

We calculated the minimum neighbor distance between occupied grid cells, using the centroids of the 1 km² cells. We tested for an effect of phenotype on these values with a t-test. To test for the presence of clusters in the distribution of the rare phenotype, we used the Nearest Neighbour Index Clustering (NNIC) algorithm, which is based on a Delaunay triangulation to identify and locate each cluster individually on the basis of a threshold distance, determined by the Nearest Neighbour Index (NNI) (Clark and Evans, 1954; Sillero, 2021) . The NNI considers a cloud of points (here, data at the finest resolution, i.e. centroids of 1 km² grid cells) to be clustered when the mean nearest neighbor distance among points is lower than the expected value (i.e., the mean neighbor distance of a random cloud of points). The NNI ranges from 0 to 2.15. A value higher than 1 indicates a regular pattern, a value lower than 1 means clustering, and a value of 1 indicates randomness (Clark and Evans, 1954). We computed the length of the lines of a Delaunay triangulation among all points, selecting those Delaunay triangles with lines shorter than the expected nearest neighbor distance (Clark and Evans, 1954). The points intersecting the selected Delaunay triangles were considered as to be clustered.

We performed the statistical analyses in R 4.1.3 (RCoreTeam, 2022) , including the Rcmdr package, and in Statistica 13.3 (StatSoft).
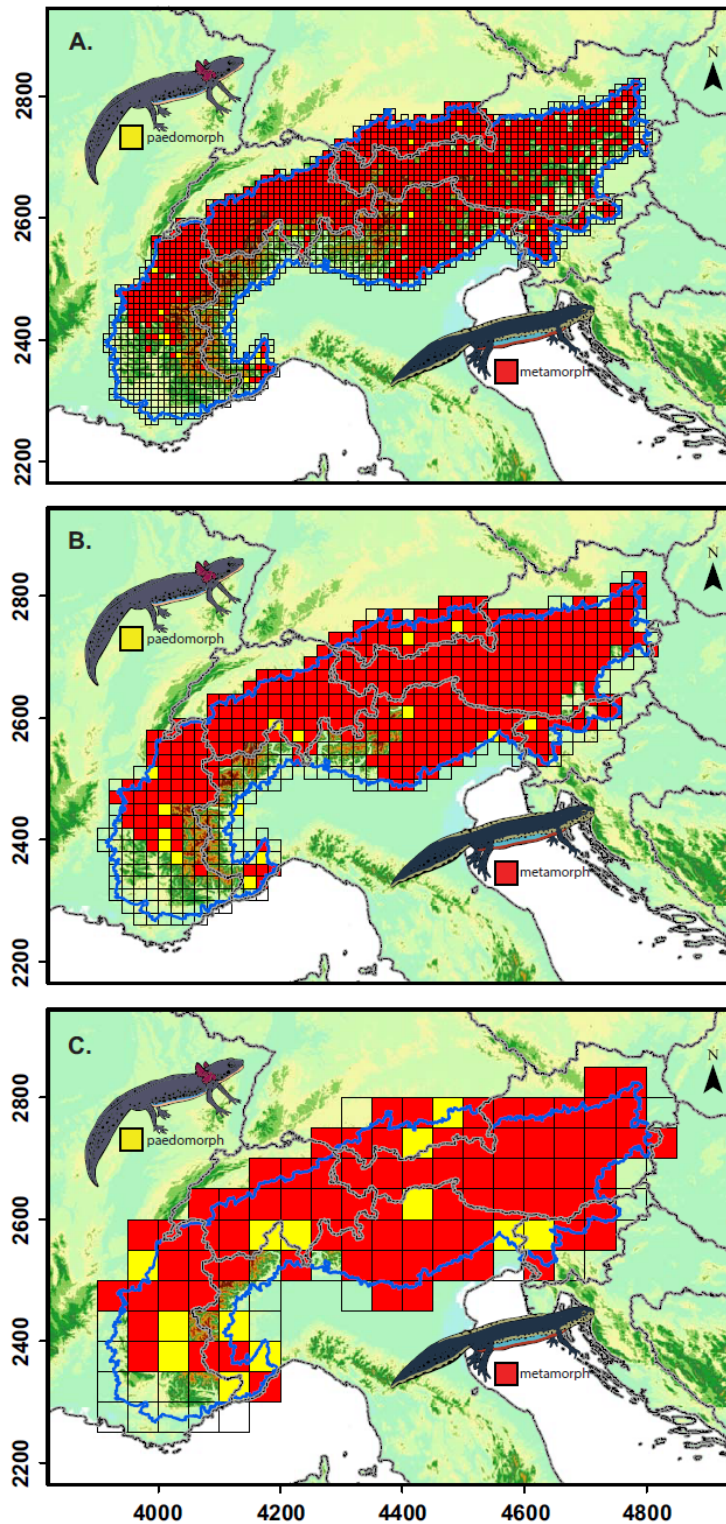
Fig. 2. Geographic distribution of two phenotypes of the Alpine newt across the Alps at three spatial scales, highlighting the rarity of paedomorphs (yellow squares) and commonness of metamorphs (red squares): (a) 10 x 10 km, (b) 20 x 20 km, (c) 50 x 50 km grid cells (European Environmental Agency grid; geographic coordinates are given in km). Metamorphs were also present in all the grid cells occupied by paedomorphs. Data are based on the combination of observation records (*n* = 15,613) from the regional and national databases of the seven Alpine countries. Grey lines: country boundaries; thick blue line: limits of the Alpine Convention. Background: digital terrain elevation (Copernicus, open data).

3. Results

3.1. General patterns

Populations of paedomorphs were found in five of the seven Alpine countries, whereas populations of metamorphs were present in all seven countries (Fig. 2; Tables A1 and A2). More specifically, paedomorphs and metamorphs, respectively, were found in 25 and 7,287 different 1 km² grid cells, the finest spatial scale used here (Fig. 3A; Table A3). This represents AOOs covering 0.01% and 3.8% of the Alps for paedomorphs and metamorphs, respectively (n = 194,009 grid cells over the Alps; Table A3). Therefore, on this basis, the populations of paedomorphs were geographically 292 times (i.e., 7287/25) less widespread than those of metamorphs at this fine spatial scale. There was a significant effect of phenotype on the area of occupancy (AOO) and the number of 1 km² grid cells used at each coarser spatial scale (Table 1). The AOO of the paedomorphs was significantly smaller than that one of the metamorphs ($P < 0.001$; Table 1, Fig. 3A, Table A3), and the number of occupied 1 km² grid cells per coarser grid cell was significantly lower for paedomorphs than metamorphs ($P < 0.001$; Table 1, Fig. 3B, Table A4). The extent of occurrence of paedomorphs was 53% smaller than that of the metamorphs (128,142 vs 239,949 km²).

3.2. Scale effects

The level of relative rarity of paedomorphs when compared to metamorphs decreased significantly as spatial scale increased (i.e., from fine- to coarse-grain resolutions) for the AOO, with scores of rarity 42 times (i.e., 292/7) lower at the broadest than at the finest spatial scale ($P < 0.001$, Table 1, Fig. 4, Table A3). There was a significant effect of spatial scale on the AOO ($P < 0.001$, Table 1). The AOO was evaluated to be 1,300 and 31 times larger at the coarsest than at the finest spatial scale for the paedomorphs and the metamorphs, respectively, which means that the areas of occupancy were estimated to range from 25 km² to 32,500 km² for the paedomorphs versus 7,287 km² to 227,500 km² for the metamorphs (Figs. 2C and 3A; Table A3). At the 4 km² grid scale, the AOO was 236 times smaller for paedomorphs than for metamorphs (i.e., 92 km² and 21,668 km², respectively). At the 100 km² grid scale, which is the finest shared spatial resolution across published national and regional atlases over the Alps, paedomorphs' AOO amounted to 1,700 km² and that of metamorphs was 119,700 km² (Fig. 2; Table A3). This means that paedomorphs were 70 times rarer than metamorphs at this spatial scale. There was a significant effect of spatial scale on the number of 1 km² occupied grid cells at each coarser grid scale ($P < 0.001$; Table 1). There were 1.8 and 48 times more occupied grid cells at the coarser than at the finer scale in paedomorphs and in metamorphs, respectively (Fig. 3B; Table A4). The AOO of the paedomorphs was from 5,126 to 4 times lower than the extent of occurrence from the finer to the coarser spatial scales (Table A5). For metamorphs, it was from 33 to only 1.06 lower (Table A5).

Table 1

Results of linear models relating the area of occupancy (AOO) and the number of occupied 1 km² atlas grid cells in larger grid cells (up to 2,500 km²) to the phenotype and the spatial scale (i.e., resolution) and the relative index of rarity between phenotypes to the spatial scale. P: paedomorph.

Dependent variable	Factor	Estimate	SE	95% CI	Test	df	P
Area of occupancy	Spatial scale	0.68	0.08	0.49, 0.87	$t = 8.022$	1,9	<0.0001
	Phenotype (P)	−1.85	0.19	−2.29, −1.41	$t = -9.52$	1,9	<0.0001
Number of cells	Spatial scale	1.92	0.015	1.89, 1.95	$z = 125.51$	1,9878	<0.0001
	Phenotype (P)	−0.61	0.10	−0.81, −0.42	$z = -6.342$	1,9878	<0.0001
Relative index	Spatial scale	−1.98	0.245	−2.47, −1.50	$t = -7.996$	1,4	0.001

3.3. Clustering

Populations of paedomorphs (considering the finest resolution) clustered significantly (Delaunay analysis: $Z = 0.519$, $P < 0.001$), highlighting a single cluster around the Dauphine Alps in France (Fig A1). The populations of paedomorphs were significantly more distant from each other than were the populations of metamorphs (30.313 ± 7.291 km and 1.698 ± 0.017 km, respectively; t-test $= 55.446$, df $= 7310$, $P < 0.001$).

3.4. Threats

Fish introductions were detected in 40 % of the waterbodies in which populations of paedomorphs were found in the Alps (Table A2). This encompassed 33%, 50%, 28%, 100% and 67% of known populations of paedomorphs in France, Germany, Italy, Slovenia, and Switzerland, respectively; this means in all Alpine countries where populations of paedomorphs were found (Table A2).

4. Discussion

Our approach of combining fine-grain data from multiple distribution and atlas databases as well as several metrics proved successful in quantifying rarity of intraspecific diversity at different spatial scales (i.e., from fine- to coarse-grain resolutions) over an entire biogeographic area, the European Alps. The analyses evidenced the need to use fine-grain data over broad geographical areas to adequately account for the level of rarity of phenotypes and consequently their level of threat. Indeed, whereas the model species as a whole can be common and widespread, its intraspecific components were not. Moreover, the level of rarity could vary by up to three orders of magnitude depending on the spatial scale for the rarest phenotype.
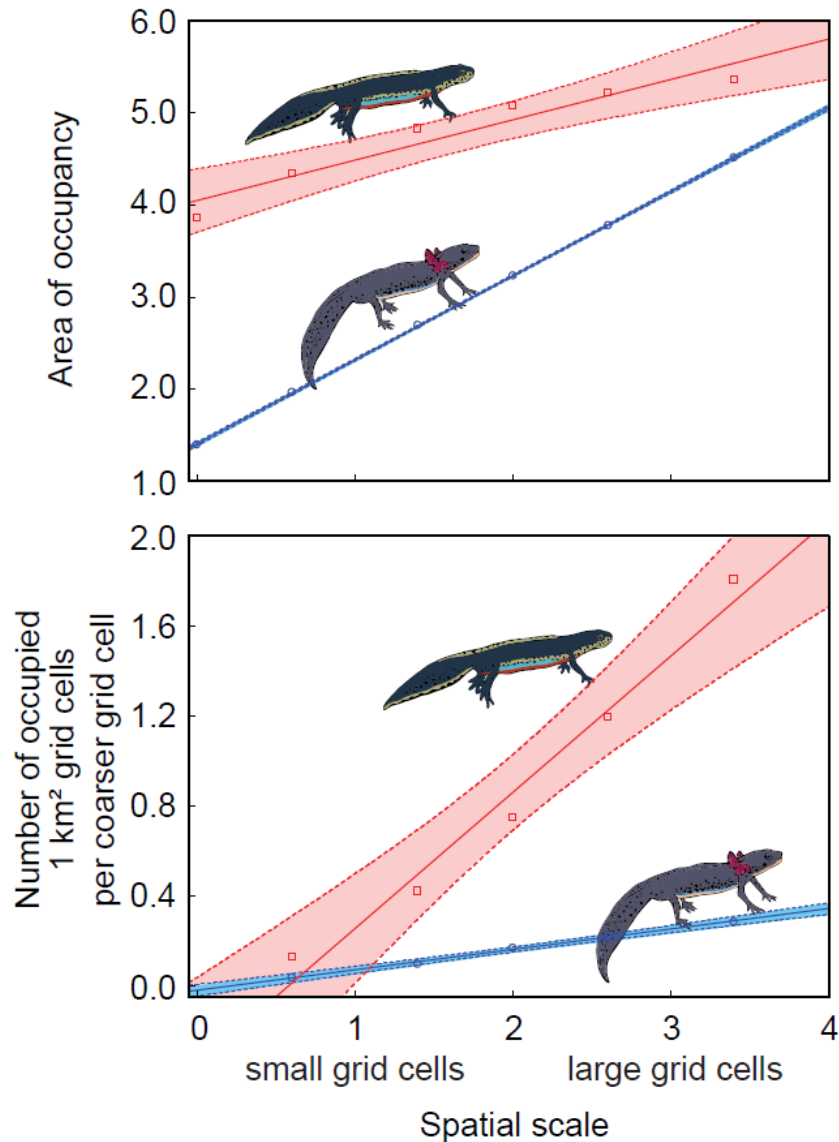
Fig. 3. Absolute rarity metrics of the rarity of the rare phenotype (paedomorphs) and the common phenotype (metamorphs) of the Alpine newt at multiple spatial scales (cell sizes of 1 to 2,500 km²) over the Alps: (a) Area of occupancy (in km²); (b) Number of occupied 1 km² grid cells per coarser grid cell in the area of occupancy. All values have been log$_{10}$ transformed. Lines: linear regressions and 95% confidence intervals; red lines and squares: metamorphs; blue lines and circles: paedomorphs.

4.1. Rarity and clustering of paedomorphosis

Intraspecific diversity, such as facultative paedomorphosis, has been previously described as more localized or rarer than the species as a whole (Denoël, 2007; Emel and Bonett, 2011). In Alpine newts, for instance, some checklists of the known populations of paedomorphs were established, but as for other species exhibiting facultative paedomorphosis, these checklists lack a point of comparison with the number of populations of the species to infer their rarity (Kalezić and Dzukiž, 1986; Andreone and Dore, 1991; Denoël et al., 2001). Here, we filled this gap by evaluating quantitatively the rarity of the rare paedomorphic

phenotype, which was 292 times rarer than the species as a whole and occupied only 0.01% of an entire biogeographic area at the finest spatial scale available (grid cells of 1 km^2). This extremely low proportion reveals that using databases enriched with citizen-based data allows for better defining rarity than when using researcher-based data alone due to underestimations of the common phenotypes (Denoël et al., 2009). Not all populations of paedomorphic newts may be known because either some sites were not surveyed or because paedomorphs were not detected in mixed populations of paedomorphs and metamorphs. However, since paedomorphic Alpine newts have been studied and attracted attention for decades, we think that the vast majority of populations of paedomorphs is known in the study area. In any case, adding a few populations would not change the results substantially.

The Alps were not previously regarded as a hotspot for paedomorphosis, but the present results show that the Alps host 26% of the populations of paedomorphs described in Europe in the study species (Denoël et al., 2001; Denoël et al., 2019b; this study). The fact that the populations of paedomorphs represented an extremely small fraction of the geographic coverage (i.e., 0.01%) confirms the Alps are not a hotspot per se for paedomorphosis. Nevertheless, by using the clustering analysis allowed us to delineate a new hotspot within the south-western part of the Alps where 39% of the populations with paedomorphic individuals have been found (Breuil, 1986; Denoël et al., 2001; Deso and Roinard, 2015; Table A2). The clustering analysis may also give a support for management programs in identifying key geographic areas for undertaking new surveys to identify new sites with paedomorphs as well as for targeting conservation action, such as those involving reintroductions, habitat restoration or the removal of non-native fish (see also Denoël and Ficetola, 2015 for other methodological approaches). Previous studies showed that populations of the paedomorph can be resilient once the threats are removed and when nearby populations still express the developmental polymorphism (Denoël and Winandy, 2015). For more isolated populations, it is yet unlikely that paedomorphs will re-appear. For instance, *Ichthyosaura alpestris lacustris*, endemic to a single isolated Alpine lake in Slovenia and where paedomorphs were described is now considered extinct (Stanković et al., 2015).

4.2. Commonness, rarity, and spatial scales

Spatial scale has been shown to affect the assessment of AOO and therefore rarity (Hartley and Kunin, 2003; Joseph and Possingham, 2008). Our results on the effect of spatial scale (i.e., resolution) in Alpine newts align with these results at the intraspecific level, yet yielded contrasting outcomes in both rare and common phenotypes. The absolute and relative rarity estimates of the paedomorphs were 1,300 and 42 times lower at the coarser scale than at the finest spatial scale, respectively. Similarly, but at a much lesser extent, the commonness of the common phenotype reached a value 31 times higher at the coarsest than at the finest spatial scale. The EOO, being close to the AOO at the coarser spatial scale, was inadequate to infer rarity, and this was particularly true for the rare phenotype. These results revealed that the effect of spatial scale was much more marked on the rare phenotype than on the common one and that EOO was not effective in assessing the rarity of the rarer phenotype. For estimating rarity, our results support the recent view that future broad-scale grid-based mapping should move to 10

x 10 km (or finer) grid cells when data availability allows for it (Sillero et al., 2014, 2018; Ambu & Dufresnes, 2022) as this will allow to describe patterns of intraspecific biodiversity more accurately.

Caution should be taken when using very fine spatial scales as this may over-estimate our perception of rarity due to false absence (Herrando et al., 2019). A trade-off has to therefore be maintained between the quantity of available data and the spatial scale used for distribution analyses. This is particularly true for absolute estimates of rarity, suggesting that relative measures could offer a valuable alternative – particularly when data availability is limited. In the Alps, the different mapping initiatives were successful in accumulating a large amount of data which resulted already in the publication of several atlases (Cabela et al., 2001; Sindaco et al., 2006; Meyer et al., 2009; Kühnis, 2011; GHRA - LPO Rhône-Alpes, 2015; Andrä et al., 2019; Schmidt and Zumbach, 2019) while the unpublished data will be used for future atlas updates and other conservation purposes. This indicates the robustness of the data on which our analyses were based. The overall quality is also exemplified by the continuous observed distribution of metamorphic Alpine newts from the western to the eastern side of the Alps (Fig. 2).
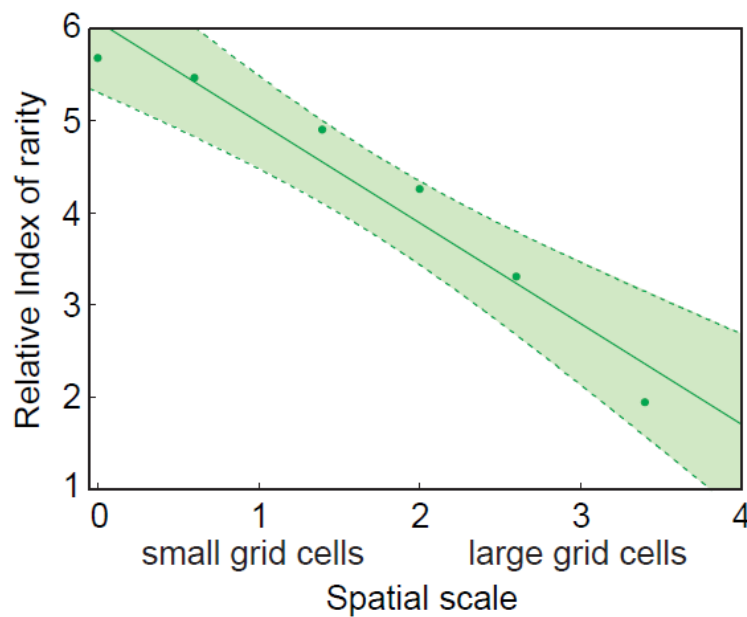

Fig. 4. Relative rarity metric of the rare phenotype (paedomorphs) on the common phenotype (metamorphs) of the Alpine newts at multiple spatial scales (cell sizes of 1 to 2,500 km²) over the Alps. All values have been log10 transformed. Dots: estimates at each spatial scale; Lines: linear regressions and 95% confidence intervals.

4.3. Threats and intraspecific rarity

Our results support the view that the Alpine newt as a whole (i.e., at the specific level) is not globally endangered, justifying the reported international status of Least Concern based on the large AOO of the species (IUCN SSC Amphibian Specialist Group, 2022). Because rarity can indeed variate geographically, applying Red List status at a regional scale can

highlight different figures than at a global scale (Schoener, 1987; Dufresnes and Perrin, 2015). In the Alps, the species is classified as Least Concern in six countries (Schmidt and Zumbach, 2005; Kühnis, 2011; Rondinini et al., 2013; Stanković et al., 2015; UICN France et al., 2015; Schulte and Thiesmeier, 2020), as Near Threatened in Austria and in the French Department of Provence-Alpes-Côte-d'Azur (Gollmann, 2007; Marchand et al., 2017; Table A6). The French department is also the area which hosts a major population of paedomorphs (see e.g. Denoël et al. 2005b, Lejeune et al. 2018) and which is close to the detected hotspot in the Dauphine Alps.

In contrast to the patterns found at the species level, paedomorphic populations were rare throughout the distribution range of the Alpine newt, a pattern described by Schoener (1987) as a "suffusive" rarity pattern. If the criteria for IUCN Red Lists were applied using AOO at the intraspecific level (i.e., beyond the current aim of IUCN Red List) and using a fine recommended spatial scale, i.e. 4 km² (IUCN, 2019), paedomorphic Alpine newts would belong to the most endangered category (critically endangered) throughout the Alps according to criterium B2 because (a) their AOO is less than 100 km², (b) there is a severe fragmentation of the populations (Table 1; Fig A1), (c) there is a persistence of threats and (d) a continuing decline (Denoël et al., 2005a; Denoël et al., 2016). Previous reports highlighted the risk of fish introductions leading to declines and extirpations of populations of paedomorphs in all Alpine countries where paedomorphs were found (Seliskar and Pehani, 1935; Henle, 1983; Breuil, 1985; Denoël et al., 2001; Deso and Roinard, 2015; Stanković et al., 2015). There are multiple possible mechanisms why paedomorphs may decline faster and more strongly than metamorphs after the introduction of fish. Among them, there is the continued presence of the paedomorphs in water throughout the year (whereas the metamorphs have the potential to escape on land; Denoël et al., 2005a; Winandy et al., 2017), the frequent use of open water where salmonids often forage (Denoël and Joly, 2001; Tiberti et al., 2017), and a more reduced reproductive fitness in the presence of fish (Denoël et al., 2019a). Here we showed that at least 40% of populations of paedomorphs were indeed threatened by fish introductions throughout the Alps. This is quite similar to what was found in Montenegro, where fish were found in 52% of water bodies initially occupied by paedomorphs (Denoël et al., 2019b). Keith et al. (2018) highlighted that the risk is also dependent on the scale at which the threat is present. As fish are limited to single aquatic water bodies, their range fits typically that one of the finest spatial scale used here or lower; giving similar assessment than the usually applied 4 km² spatial scale (IUCN, 2019). Considering scales of 1 or 4 km² remains yet pertinent in terms of conservation because the resilience of paedomorphs relies on the presence of metamorphs, which can live on land until fish disappear from waterbodies (Denoël and Winandy, 2015). If any other coarser spatial scales were applied than the finer spatial scales (1 or 4 km²), by using the same B2 criterium (IUCN, 2019), paedomorphic Alpine newts would have been considered as endangered (25 km² spatial scale), vulnerable (100 and 400 km² spatial scales) or only near threatened (2,500 km² spatial scale). Using coarse spatial scales may therefore hide rarity and threat level patterns (see also IUCN, 2019). Finally, the effects of climate change on the populations of paedomorphs need to be evaluated as previous experimental research showed detrimental effects of water availability on paedomorphic Alpine newts (Denoël, 2003; Mathiron et al., 2017). On the other hand, an increase of aridity may also favor paedomorphosis by counter-selecting terrestrial metamorphosed individuals, provided that the aquatic habitat remains suitable (Bonett et al,

2014) and by removing fish, provided the descendants of metamorphs can still express paedomorphosis (Denoël & Winandy, 2015).

We can learn two main lessons from these findings. First, polyphenisms and more generally intraspecific diversity should not be neglected in Red Listings, legislation and conservation programs so to allow effective protection of rare intraspecific diversity. This is an important aspect because conservation managers and administrations are using the Red List status at the species level – what it is primarily done for – and thus could overlook the risk of intraspecific biodiversity loss. Most of concerns on intraspecific diversity in the literature refers to genetic diversity, including when it refers to polymorphisms (see e.g. Hindar, 1994, Degner et al. 2007; Thakur et al. 2018) which is yet rarely implemented in international conservation policy (see e.g. Hoban et al. 2021). Phenotypic differentiation and more specifically polyphenisms, such as facultative paedomorphosis, have rarely been the focus of conservation concerns and are not yet considered in conservation policy (Denoël et al., 2005a; Bush and Adams, 2007; Denoël, 2007; Taylor et al., 2011; Denoël and Ficetola, 2015). Similarly, some Red Lists integrate subspecies (Haig et al., 2006; Gippoliti and Amori, 2007) but a further step is still needed to include polyphenisms. Second, fine-scale analyses of distribution can help determining Red List criteria for intraspecific diversity and allows to figure out rarity across spatial scales; thus helping to orient conservation programs to adequate spatial scales. Although used here for a polymorphism, such analyses could be processed for all intraspecific patterns of diversity.

4.4. Conclusions: Rarity and the value of citizen science data

Our assessment of rarity of intraspecific diversity would not have been possible without citizen-based distribution data at the species level. Monitoring and survey programs involving volunteers are therefore useful and essential for the efficient quantification of distribution and population trends (Bonardi et al., 2011; Moor et al., 2022) and to evaluate rarity at intraspecific level, as shown here. The most detailed data sets come from regional and national initiatives that collect, classify, and validate distribution data (i.e., presence records). In the present study, all Alpine countries had their own independent distribution atlas programs. This was an asset in providing complete coverage at a fine spatial scale (i.e., resolution) but also posed a challenge due to the enforcement of confidentiality rules. Future cooperation among database providers will be the key to extending the present approach to multiple taxa and other geographic areas. This will be particularly helpful to highlight the rarity levels of intraspecific diversity in other animal groups. This will not only be useful for quantifying rarity levels but also for highlighting where rarity is the rarest (Rodrigues and Gaston, 2002; McLean and Stuart-Fox, 2014), as well as to target conservation measures in transboundary protected areas efficiently (Zimmerer et al., 2004). These programs have already been proven efficient from local to regional and national fine spatial scales and at continental, coarse spatial scales (Sillero et al., 2014), but mapping and rarity assessments at a high resolution over a broad geographic extent are now needed to understand rarity at both the species and intraspecific levels.

CRediT author statement:

Mathieu Denoël: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation; **Mathieu Denoël and Neftalí Sillero:** Data curation and Formal analysis; **Mathieu Denoël, Benedikt R. Schmidt, Rémi Fonters, Günter Hansbauer, Aurélie Johanet, Jürgen Kühnis, Katja Poboljsaj, Silke Schweiger:** Data acquisition and processing; **Mathieu Denoël:** Writing - original draft; **Mathieu Denoël, Benedikt Schmidt and Neftalí Sillero:** Writing - review & editing; all authors: agreeing with the final version of the manuscript.

Appendix A. Supplemental data

Supplementary data to this article can be found online

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