

Herps without borders: a new newt case and a review of transalpine alien introductions in western Europe

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Abstract. Biogeographic processes have led to different evolutionary taxa occurring in the northern and southern edges of the Alpine Mountains in Western Europe. The integrity of this diversity is being challenged by frequent human-mediated trans-alpine translocations, sometimes leading to biological invasions. Several alien terrestrial vertebrates of south Alpine origins (Italy, Swiss Ticino) are causing damages to native north Alpine fauna. In this paper, we used molecular tools to characterize the understudied case of the Mediterranean smooth newt (*Lissotriton vulgaris meridionalis*) expanding in the outskirts of Geneva since its introduction before 1975. Mitochondrial and nuclear DNA sequencing suggest that these exotic populations are a mixture between two diverged *L. v. meridionalis* lineages from central Italy, and traces of potential hybridization with the native *L. v. vulgaris* was detected. This situation echoes many other trans-alpine alien introductions. We review all comparable cases of southern to northern Alps introductions in vertebrates, including seven reptiles and four amphibians. The majority of south alpine alien lineages were presumably imported voluntarily by enthusiasts and appear to perform better in the disturbed habitats found in the anthropogenic landscapes of Western Europe compared to their native north Alpine counterparts. Most pose serious threats to related species of similar ecology, through direct competition, predation and introgressive hybridization. Difficulties to detect alien species on time lead to significant conservation costs. Better education together with more appropriate and reactive management plans will be necessary to limit the impact of future alien introductions.

Keywords: Alps, amphibians, biological invasions, conservation, herpetofauna, Italy, *Lissotriton vulgaris*, reptiles.

Introduction

Improper education, legislation, care and knowledge regarding species distinctions and distributions, combined with increased globalization, have promoted a myriad of uncontrolled faunal translocations over the last century (reviewed in Pimental et al., 2001; Hulme et al., 2008; Keller et al., 2011; Lowry et al., 2013; Kraus, 2015). In many instances, these events led to the establishment of sustainable alien

populations that have eventually become invasive, with significant bioeconomic costs (Keller et al., 2011). The main threats posed to biodiversity include predation, competition, transmission of diseases and hybridization with native species resulting in genetic pollution potentially inducing local extinctions. Confusion between closely-related alien and native taxa is a serious shortcoming to management of introduced populations. For this reason, genetic tools are now instrumental to guide conservation efforts (Chown et al., 2014; Cristescu, 2015). Invasion genetics can further inform on the scenario and origins of introductions, a crucial step for adjusting legislative efforts and raising awareness towards the responsible parties (Chown et al., 2014; Cristescu, 2015).

In continental Europe, biogeographic processes affected terrestrial vertebrates by driving evolutionary divergences between Italian, Balkan and Iberian populations, which have often reached specific or subspecific taxonomic levels (Schmitt, 2007). While Balkan

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and Iberian populations expanded their distribution ranges to Central and Northern Europe after the glaciations, many lineages with Italian glacial refugia remained restricted south of the Alps, and are therefore endemic to the Apennine Peninsula (Sillero et al., 2014). Hence, in many taxa, the northern and southern slopes of the Alps are inhabited by distinct evolutionary lineages, naturally isolated by the Alpine arc. However, frequent trans-Alpine translocations (i.e. between the southern to the northern sides of the mountains) have considerably challenged the integrity of natural distributions. Multiple Italian species have been successfully introduced northward in Switzerland, Germany and the Benelux countries, sometimes with significant conservation damages (table 1; reviewed in the Discussion section).

An understudied case of transalpine introduction is the smooth newt (*Lissotriton vulgaris* sp. complex) from the area of Geneva, Western Switzerland. The *L. vulgaris* radiation is a diverse species group with nine lineages distributed throughout the Balkans, Anatolia, as well as northwestern and central Europe. The taxonomic position of many of them is unclear and is currently being revisited following molecular studies (Babik et al., 2005; Pabijan et al., 2015; Pabijan et al., 2017). Notably, several taxa were proposed a specific status given reciprocity of nuclear and mitochondrial divergence, disruptive geographic range and narrow transitions (Pabijan et al., 2017; reviewed in Wielstra et al., 2018). One lineage, the Mediterranean smooth newt, *L. v. meridionalis* (recognized as a distinct species by some authors), is widely distributed from the Adriatic coast (Slovenia and Croatia) through Central and Northern Italy (Maura et al., 2014). While Switzerland naturally hosts *L. v. meridionalis* in Ticino, the north-alpine parts of the country are inhabited by the nominal subspecies *L. v. vulgaris*. Both taxa are found in lowland damp meadows and various types of ponds. They can be distinguished by the shape of their dorsal

fin (wavy in *L. v. vulgaris*: “ragged crest” phenotype; straight in *L. v. meridionalis*: “smooth crest” phenotype; Raxworthy, 1990).

Smooth newts with typical *L. v. meridionalis* phenotypes were introduced in the outskirts of Geneva, Western Switzerland, at least prior to 1975, and have since colonized >30 ponds throughout the Canton (JT, pers. comm.). The origin and authors of these releases are unclear. While the autochthonous *L. v. vulgaris* does not occur in this area, the expansion of alien *L. v. meridionalis* combined with the invasive potential of this species group (Tingley et al., 2015) is worrisome, and an eradication program has been initiated by relevant authorities and local societies.

In this study, we apply mitochondrial and nuclear markers to confirm the nature of alien *L. v. meridionalis* in Geneva, pinpoint its geographic origin(s) and understand the scenario of introduction, using the detailed phylogeographic framework provided by Maura et al. (2014) as a reference. More globally, we provide insight into why this specific pathway of introduction is so successful by reviewing all known transalpine translocations in vertebrates, and draw lessons for future situations.

Material and methods

Sampling

A total of 20 *L. vulgaris* specimens were collected during Spring and Summer 2017 (fig. 1; details in supplementary table S1): 14 covering the known introduction area (Geneva canton), 4 from natural *L. v. meridionalis* populations from Swiss Ticino (a potential source area), and 2 from a western Swiss natural reserve hosting the autochthonous and threatened *L. v. vulgaris* (Grande Carrière). DNA was obtained from tail tips or buccal swabs and extracted using the Qiagen Blood & Tissue kit.

Genotyping of mitochondrial and nuclear markers

We genotyped two mitochondrial markers, ND2 (~1000 bp) and ND4 (~800 bp) in 19 samples using the primers and methods described in Babik et al. (2005). These markers have been widely used in several comprehensive phylogenetic and phylogeographic studies on the *L. vulgaris* radiation (Babik et al., 2005; Pabijan et al., 2015; Pabijan et

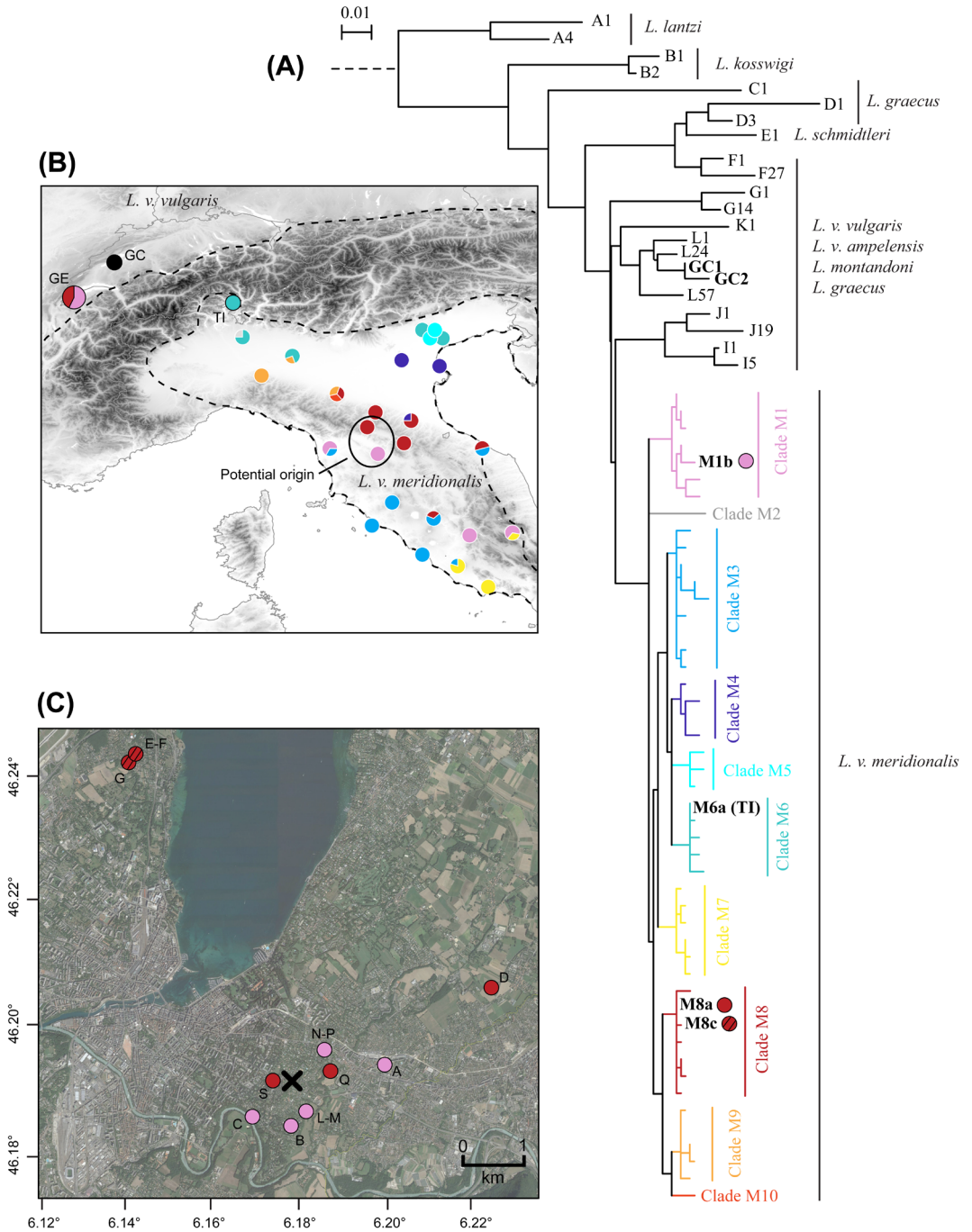


Figure 1. (A) Mitochondrial phylogeny of *Lissotriton vulgaris* spp, (B) distribution of lineages and (C) distribution of the three haplotypes found in the canton of Geneva. Colors correspond to the clades of *L. v. meridionalis* identified by Maura et al. (2014). Samples from this study (black frames) include the Geneva area (GE, haplotypes M1b, M8a and M8), Ticino (TI, haplotype M6a) and the Grande Cariçaie from Western Switzerland (GC, haplotypes GC1 and GC2). For (C), letters correspond to the specimen sampled, and the cross indicate the presumed point of origin of the invasion in Geneva. For (C), Latitude (N) and Longitude (E) are indicated in decimal degrees.

al., 2017), particularly on *L. v. meridionalis* where the fine-scale distribution of haplogroups is well-known (Maura et al., 2014).

Furthermore, in order to assess the nuclear identity of our samples, we sequenced ~600bp from the nuclear gene *Sodium-calcium exchanger 1 (Ncx1)* in 7 *L. vulgaris* individuals (3 from Geneva, 2 from Ticino, 2 from the Grande Carîçaie Nature reserve), using primers and methods from Nadachowska and Babik (2009). Because publically-available data for *Ncx1* is not exhaustive for *Lissotriton* and other sympatric newt species, we also sequenced samples from other newts present in Geneva, namely *Lissotriton helveticus* ($n = 2$), *Ichthyosaura alpestris* ($n = 2$) and *Triturus carnifex* ($n = 1$), available from other studies (Dufresnes et al., 2016; GL, unpublished data).

Phylogenetic analyses

Our mitochondrial data was concatenated (ND2 + ND4), trimmed down and aligned with the 47 *L. v. meridionalis* concatenated haplotypes from Maura et al. (2014) and the 21 *L. vulgaris* concatenated haplotypes from Babik et al. (2005), covering the entire radiation, for a total of 1294bp. We matched our haplotypes to published ones and visualized genetic divergence by building a maximum-likelihood phylogeny with PhyML (Guidon and Gascuel, 2003), using a GTR + G + I model of sequence evolution (jModelTest, Darriba et al., 2012). Published sequences from *L. helveticus*, *L. italicus* and *L. boscai* (Babik et al., 2005), the closest relatives to the smooth newt radiation, were used as outgroups.

Our nuclear data was trimmed and aligned with published *Ncx1* sequences. These included haplotype sets from *L. schmidleri* and *L. kosswigi* (Nadachowska and Babik, 2009), and individual sequences from *Triturus marmoratus* and *Calotriton asper* (Roelants et al., 2007). Like for mtDNA, we visualize genetic variation with a maximum-likelihood reconstruction using a GTR + G + I model of sequence evolution. Given the low polymorphism of *Ncx1* (see Results), sequences from distantly related taxa (*Salamandra salamandra*, *Proteus anguinus* and *Speleomantes italicus*) were used as outgroups.

Results

We found three mitochondrial haplotypes among introduced newts from Geneva, corresponding to two distinct *L. v. meridionalis* lineages co-occurring in Central Italy, namely clade M1 and M8 from Maura et al. (2014; fig. 1A and 1B). Among our 14 individuals, 8 possessed haplotype M1b (individuals A-C, L-P), 3 possessed haplotype M8a (individuals D, Q and S) and 3 possessed haplotype M8c (individuals E-G), all previously reported (Maura et al.,

2014). Interestingly, the latter three were collected from a remote pair of ponds located north of the Rhône River, suggesting some local genetic structure (fig. 1C).

Our three reference *L. v. meridionalis* from Ticino all harbored haplotype M6a, belonging to the proximate northeastern Italian clade M6 (fig. 1A and 1B). Finally, our analyses confirmed that individuals from the Grande Carîçaie nature reserve belong to the Western-European *L. v. vulgaris* L clade from Babik et al. (2005); their haplotypes (GC1 and GC2) were, however, not found in previous studies, which lacked Swiss samples.

Two smooth newts from Geneva (individuals M and S) harbored a single nuclear haplotype, also sequenced from the *L. v. meridionalis* reference samples from Ticino, named here MER1 (fig. 2). The *L. v. vulgaris* individuals from the Grande-Carîçaie nature reserve accordingly featured a different haplotype, diverged from the *L. v. meridionalis* MER1 by one mutation, and hereby named VUL1 (fig. 2). The third smooth newt sequenced from Geneva (individual G) was heterozygous; tentative phasing could separate the common MER1 allele from a second allele clustering with *L. v. vulgaris*, but featuring three singletons (named VUL2). Interestingly, this individual inhabited one of the remote ponds surveyed north of the Rhône, where a different mtDNA haplotype M8c is present.

Discussion

Lissotriton vulgaris meridionalis in Geneva

Our results confirm the presence of exotic Mediterranean smooth newts throughout the canton of Geneva, most likely originating from Central Italy. The occurrence of two distinct mtDNA lineages either suggest independent releases from different Italian sources, or, most likely, imports from a single area, Tuscany/Emilia-Romagna, where these lineages naturally meet and most likely admix (fig. 1). The reasons of these releases are unknown but

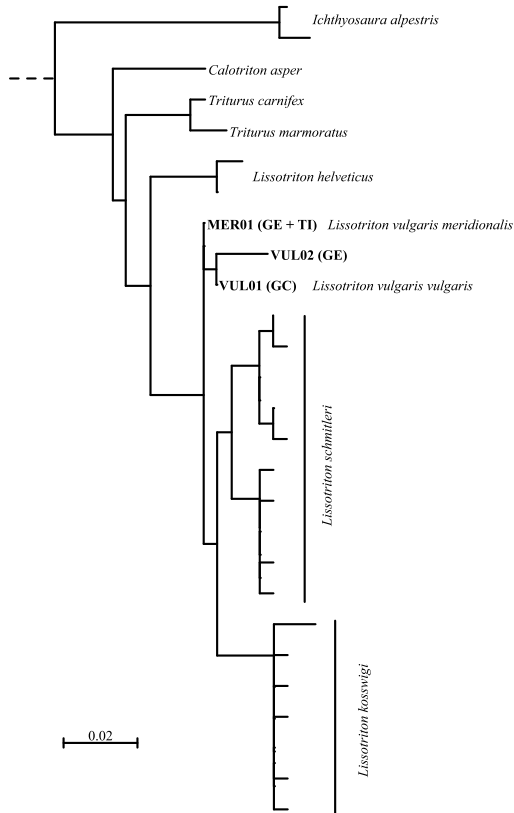


Figure 2. Nuclear phylogeny of *Ncx1* for *Lissotriton* and other newts. Haplotypes found in Geneva (GE) are MER01 (*L. v. meridionalis* also sequenced in Ticino, TI) and VUL02 (related to *L. v. vulgaris* haplotype VUL01 sequenced from Western Switzerland in the Grande Carrière nature reserve, GC).

may involve herpetological enthusiasts or researchers, newts being a popular home and lab pet; a former experimental station of a zoological institute is located close to early observations of the introduction. In at least four decades, alien newts propagated and established sustainable populations over more than 30 sites throughout the canton, through natural or human-mediated dispersal.

The isolated population sampled north of the Rhône (represented by our individuals E-G) provided more puzzling results. The different mtDNA haplotype fixed there (M8c) testifies of some local genetic structure, which is surprising given the short time-scale of the invasion. Such structure may result from drift, following

subsequent translocations from the main area of introduction south of the Rhône (in which case M8c may also locally occur there). Significant genetic structure can arise at short geographic and time scale in thriving invasive populations (Short and Petren, 2011; Schulte et al., 2013). Alternatively, these populations, established as early as the 1980s, might be the product of independent releases involving a different Italian source; because haplotypes M8c and M8a co-occur in natural ranges, it will however be difficult to disentangle these hypotheses. Moreover, the presence of a *L. v. vulgaris*-like nuclear allele in individual G might stem from hybridization with native smooth newts, although no population are known nearby. Yet, this allele may also stand from incomplete lineage sorting of *Ncx1*, especially since *L. v. vulgaris* and *L. v. meridionalis* diverged recently, with the former being paraphyletic in Western Europe (Pabijan et al., 2017); assessing introgression will require additional reference samples and loci. If it does occur, introgressive hybridization could have devastating effects on native *L. v. vulgaris* (listed as endangered on the Swiss Red list of amphibians), especially given the rate of propagation of alien *L. v. meridionalis* observed in Geneva. In this way, the Italian crested newt *Triturus carnifex*, introduced in Geneva for research, has almost completely wiped out the native *T. cristatus* from Western Switzerland (Dufresnes et al., 2016; see next section). Moreover, *L. v. meridionalis* may also compete and eventually hybridize (Johanet, Secondi and Lemaire, 2011) with another threatened amphibian present in Geneva and adjacent areas, the palmate newt *Lissotriton helveticus* (“vulnerable” on the red list of Swiss amphibians). More generally, introductions are often of mixed origins in European salamandrids, as also exemplified by alpine newts (*Ichthyosaura alpestris*) from southern France (Arntzen et al., 2016).

Cases of trans-alpine introductions in amphibians and reptiles

The introduction of Italian smooth newts in Geneva adds to a long list of northwards translocations across the Alpine arc, and calls for an assessment of similar situations, particularly to understand why this regional pathway is so common. To our knowledge, eleven identified Italian vertebrate taxa, all amphibians and reptiles, were successfully introduced north of the Alps, multiple times for several of them. In the following, we review known cases and tentatively enunciate the factors that potentially paved the success for these introductions. Finally, we discuss aspects that may limit their impact and prevent new ones in the future. Note that these well-documented cases may only represent the tip of the iceberg, and that numerous translocations across Europe have potentially remained undetected so far, for reasons discussed in the following sections.

In amphibians, an old case is the Italian green frog *Pelophylax bergeri*. While the European green frog *P. lessonae* is native to Western Europe, molecular analyses evidenced that most of France and Switzerland, as well as parts of Germany, have been cryptically invaded by the Italian endemic *P. bergeri*, most likely originating from Central Italy (Dubey, Leuenberger and Perrin, 2014; Dufresnes et al., 2017). Given the extent of this invasion, the first introductions are probably quite ancient; *P. bergeri* is already present among museum samples from the 1960s (Dufresnes et al., 2017). It may very well date back to the antiquity when trade routes flourished among the Roman Empire, or more recently during the industrial revolution, which have similarly favored the expansion of non-indigenous amphibians of North-African origins over large parts of France and Spain, respectively tree frogs (*Hyla meridionalis*; Recuero et al., 2007) and painted frogs (*Disgoclossus pictus auritus*; Vences et al., 2014). Since then, *P. bergeri* has massively replaced *P. lessonae* through introgressive hybridization, and the actual taxonomic nature of

current populations is a matter of debate. In particular, green frogs form hybridogenetic complexes with another group of invasive *Pelophylax* species, the marsh frogs, *P. ridibundus* sensu lato (imported from Eastern Europe and Asia Minor for commercial purpose), further complicating the situation (Dubey, Leuenberger and Perrin, 2014; Dufresnes et al., 2018). Notably, native *P. lessonae* used to co-exist with the native hybridogenetic hybrid *P. esculentus*, which similarly lost its original gene pool following hybridization with *P. bergeri*. While long-term conservation efforts have been spent on green frogs, thus involuntary protecting the exotic *P. bergeri*, in Switzerland, programs should be redirected towards the last “pure” *P. lessonae* populations, located in remote areas that have not yet been reached by *P. bergeri* or other non-native *Pelophylax*.

The Swiss tree frogs (*Hyla*) make another interesting case of trans-alpine anuran translocation with direct conservation consequences. In the 1950s, tadpoles collected south of the Alps in Ticino were massively released by herpetologist enthusiasts in the nature reserve of the Grangettes (eastern end of Lake Geneva), in an attempt to support the local population of *Hyla arborea* (J. Garzoni, pers. comm.). However, south-Alpine tree frogs are now known to belong to a distinct species, *Hyla intermedia* and multilocus analyses showed that the recent Grangettes population is a hybrid swarm where only *H. arborea* × *H. intermedia* hybrids subsist (Dufresnes et al., 2015). Despite important and costly efforts of habitat restoration, the tree frogs of the Grangettes have kept collapsing and no individual has been reported since 2015. Given the level of reproductive isolation between the two species (which barely admix in their natural contact zone), it is plausible that hybridization and subsequent genetic incompatibilities between their genomes (usually expressed in backcrosses, i.e. hybrid breakdown), was a main driver of the potential extinction of this highly protected population (Dufresnes et al., 2015).

In newts, the case treated in this paper may involve private parties and/or an academic institute for the releases of Mediterranean smooth newts (*Lissotriton vulgaris meridionalis*) in the outskirts of Geneva before the 1980s, most likely originating from Emilia-Romagna or Tuscany. Since then, the taxon has spread across the canton and, if not stopped, may threaten the palmate newt *L. helveticus*, as well as its native counterpart *L. v. vulgaris*, respectively listed as vulnerable and endangered in Switzerland. This Mediterranean invader seems particularly successful in such an urban area and might also become invasive in other biotopes.

As briefly mentioned above, the latter case is reminiscent of an almost identical situation from a century ago, involving crested newts (*Triturus* spp.). In the early 1900s, the Italian taxon *T. carnifex* was imported from Central Italy (possibly Tuscany) presumably by the University of Geneva for zoological research (Arntzen, 1999; Arntzen and Thorpe, 1999; Dufresnes et al., 2016). Like *Lissotriton*, it quickly expanded throughout the canton and has since spread along the shores of Lake Geneva, hybridizing and replacing the native species *T. cristatus*, one of Western Europe's most declining amphibian. Similarly, *T. carnifex* appears tolerant to disturbed ponds, which might explain its success over *T. cristatus*. Potential asymmetric fitness in *T. cristatus* × *T. carnifex* cross stemming from partial reproductive isolation might also contribute, as in other crested newts (Arntzen et al., 2009). However, *T. carnifex* dispersal in Western Switzerland likely relies partly on local human-mediated translocations (pet releases, garden ornaments, etc.). Invasions by *T. carnifex* are also known from the Netherlands, originally released by a pet store in the 1970s. Aside from direct competition, expansion of *T. carnifex* is threatening local *T. cristatus* by genetic pollution and the two species currently form an artificial hybrid zone (Meilink et al., 2015). Other cases of *T. carnifex* introductions are known from the UK (imported/bred by herp breeders since the early 20th century)

(Brede et al., 2000), and southwestern Germany (release of larvae by amateur herpetologists in the 1990s; Franzen, Gruber and Heckes, 2002), where the species dispersed outside its release sites.

The best-studied case of self-sustainable trans-alpine reptile introductions is the wall lizard, *Podarcis muralis*. Mediterranean subspecies have successfully colonized several areas of Europe and North America, with >150 known populations (Schulte, 2008; Schulte et al., 2012; Schulte, Veith and Hochkirch, 2012). In northern Europe, notably the UK, Germany, Austria and Switzerland, multiple evolutionary lineages, most of North Italian origins (Southern Alps, Tuscany, Romagna, Venetia; subspecies *P. m. maculiventris*, and *P. m. nigriventris*) have been introduced over the last century, usually with very few founders (<20 individuals) (Schulte, Veith and Hochkirch, 2012). While first records are older than 1900, many new populations have been discovered in the past decades, either released by amateur herpetologists or involuntarily imported as cargo by railway traffic. Beyond direct competition, one of the main impacts is genetic assimilation of local *P. muralis* through massive introgressive hybridization (Schulte, Veith and Hochkirch, 2012).

Another wall lizard, *Podarcis sicula*, native to Italy, has also been introduced worldwide. Outside its natural range, it is known from many North American, European and Asian localities. While some introductions predate modern times (e.g. Minorca), in northwestern Europe the species was passively transported during the 20th century, notably to Germany (1913 and later extinct; together with imported trees; Schulte and Gebhart, 2011), Switzerland (1980s, *P. s. campestris*, found close to a zoo and a railway station; Schulte and Gebhart, 2011), France (together with olive trees; Pascal, Lorvelec and Vigne, 2006), and the UK (2010, imported with cargo and successfully eradicated; Hodgkins, Davis and Foster, 2012). Multiple origins are involved (Silva-Rocha et al.,

2014). The detrimental impact of this species on native fauna is unclear. It does not seem to hybridize with local taxa but likely competes with local *P. muralis*.

Italian snakes are also well represented among north alpine herps. Grass snakes with southern mitochondrial lineages (*Natrix natrix helvetica* from Italy, *N. n. persalcyprica*, from Eastern Europe or Anatolia/Cyprus), have established a successful population in Western Switzerland, close to a reptile park from which animals escaped in the 1970s (Dubey et al., 2017). While hybridization with local grass snakes is possible, the genetic nature of surrounding populations, together with the extent of the introduction, is pending further analyses.

In Switzerland, the most famous *Natrix* invader is the dice snake (*Natrix tessellata*), naturally distributed over the Italian Peninsula, the Balkans and Asia Minor. This water-associated species was relocated within Switzerland in four Swiss lakes, by reptile enthusiasts. Tens of founders were originally imported to Lake Geneva from the Maggia Valley and Lake Lugano in Ticino, as early as 1925 and again during the 1950-1960s (Mebert, 2011; Dubey et al., 2015). The species has since successfully spread locally and now actively threatens the native *N. maura*, the most endangered snake in Switzerland, by competition for food and habitat (Dubey et al., 2015; Metzger, Christe and Ursenbacher, 2011). Measures to eradicate *N. tessellata* are ongoing since 2007. The dice snake also forms isolated populations in northwestern Germany, however considered native and genetically related to Central-European populations (Guicking, Joger and Wink, 2009).

The whip snake *Hierophis viridiflavus* has a Mediterranean distribution but the N-Italian subspecies *H. v. carbonarius* has been illegally introduced in Western Switzerland (Gryonne River in Chablais) from Ticino by enthusiasts (B. Gentizon, pers. comm.), and can now be

found more than 30 km away from its introduction site. The whip snake predates on other reptiles (lizards and snakes), birds and small mammals, and as such strongly threatens some local species. An eradication program has been initiated in 2016.

In Switzerland, the north-Alpine presence of the Aesculapian snake (*Zamenis longissimus longissimus*), a thermophile lowland Mediterranean species, has always raised suspicion among herpetologists. Genetically related to North Italian snakes, these populations may stem from deliberate introduction by the Romans; alternatively, they may be the remnant of a past wider distribution when the European climate was warmer (Musilova et al., 2010). Other remote north-Alpine populations (Germany and Denmark, extinct in the latter) are of Central European descent. Two confirmed exotic populations of <100 individuals, in Wales and in London, results from zoo escapes in the 1960s and 1980s respectively. Without tangible evidence, we then do not treat this species as a successful case of human-mediated trans-alpine introduction.

The story of the European pond terrapin (*Emys orbicularis*) is not well resolved. This turtle used to be consumed by humans during the Middle Age and the native *E. o. orbicularis* subspecies supposedly became extinct in some regions (Parent, 1979; Schneeweiss, 1997; Lenk et al., 1999; Fritz, 2003). In Switzerland, it was reintroduced since the 1950s by enthusiasts from multiple sources, including “native” and non-native lineages, not representing relict populations (Raemy, Monney and Ursenbacher, 2013). In particular, the North Italian subspecies *E. o. hellenica*, originating from the Pô plain was successfully established in the area of Geneva from a few founders. In addition to direct competition, it has massively dissolved the other genomes present through hybridization, including “native” *E. o. orbicularis* and another subspecies *E. o. galloitalica*, introduced at the same time from southern France (Raemy, 2017). Parapatric subspecies

frequently hybridize in this taxon (Raemy et al., 2017). Further north, *E. orbicularis* was (re)introduced in Belgium, Luxemburg and the United Kingdom but their origin is not clear and not necessarily south-Alpine. In addition to its trade, this species remains a popular pet for herpetologist breeders, which has led to multiple translocations across Europe.

To our knowledge, there are no comparable cases in other vertebrate groups in Europe. Most invasive mammals, birds, and fishes originated from America, Asia, Africa or elsewhere in Europe (notably Eastern Europe). The few south alpine taxa recently discovered inside or north of the Alps were probably native populations that had been overlooked until recently (e.g. the Mediterranean mole *Talpa caeca*; Marchesi et al., 2000), with a few possible exceptions in Orthoptera (e.g. Pankratius, 2004; Glaw, 2009; Baur and Güttinger, 2013).

Factors enabling successful trans-alpine introductions

All confirmed Italian terrestrial vertebrates unwanted north of the Alps are amphibians and reptiles. Most releases were intentionally carried out by experienced people, i.e. researchers and wildlife enthusiasts (e.g. captive breeders), supposedly educated towards conservation issues (table 1). Yet, the identity of many cryptic species, however, was not known until the late 20th century. Still, the former generation of biologists used to welcome exotic species as an increase of north-Alpine biodiversity (e.g. Escher, 1972). Similarly, “fauna improvement” is one major cause of release for exotic herps in Europe (Hulme et al., 2008; Kark et al., 2009), as it is in other popular animals like butterflies (e.g. Gernber, 2015). Another deprecated ideology is the lack of consideration for intra-specific variation when assessing native versus non-native status of populations. Moreover, necessary precautions are not always made to prevent escapes (a major global factor, Kark et

al., 2009), by lack of caring or by the misconception that local releases have negligible impact. Beyond initial releases, both amateur herpetologists and regular citizens are responsible for propagating some alien species at the local scale, which would not disperse otherwise in modern landscapes due to habitat fragmentation (e.g. *Lissotriton*, *Triturus*, *Natrix tessellata*).

While legislation has improved to limit wildlife trade, international transport and illegal releases, enforcing them is a utopia in the current context of European globalization and connectivity, especially with open political borders (Keller et al., 2011). In Switzerland, many taxa were simply relocated within the country, originating from south of the Alps in Ticino. In addition, European legislation primarily aims at limiting the harvesting of threatened taxa (based on the CITES, i.e. the Convention on International Trade in Endangered Species), which does not concern the thriving aliens introduced north of the Alps. Their restricted exotic ranges and specific impact, limited to ecologically or genetically similar indigenous taxa, neither include them among global efforts against invasive species, as promoted by the CBD (Convention on Biological Diversity) implementing the IAS (Invasive Alien Species) actions; among the aliens reviewed here, only one, *Podarcis sicula*, is listed on the Global Invasive Species Database (<http://www.iucngisd.org/gisd/>). The efficiency of these instruments is anyhow doubtful, notably due to the diversity of national approaches regarding invasive species management and their lack of collaboration (Keller et al., 2011). In addition, the difficulty to detect some aliens, the lack of political and ethical will to eradicate exotic populations, especially when taxonomic levels are debated and when hybrids are involved (Allendorf et al., 2001), together with the involuntary help sometimes provided by misguided conservation programs (see below), have left time and opportunity for south-Alpine invaders to successfully establish and expand.

Table 1. Confirmed cases of transalpine alien introductions in terrestrial vertebrates, and their conservation impact.

Alien taxon	Origin	Introduced range	History	Conservation impact	References
<i>Hyla intermedia</i>	Ticino	W-Switzerland (extinct)	Introduced in the 1950s by enthusiasts	Genetic pollution and local extinction of native <i>H. arborea</i>	1
<i>Pelophylax bergeri</i>	Central Italy	W-Europe	Introduced prior to the 1960s	Genetic pollution, competition and replacement of native <i>P. lessonae</i> and <i>P. esculentus</i>	2-3
<i>Triturus carnifex</i>	N-Italy	Switzerland, Germany, Netherlands, UK	Introduced in the 1900s by researchers (Switzerland), in the 1970s by a pet breeder (UK) and 1990s by enthusiasts (Germany)	Genetic pollution, competition and replacement of native <i>T. cristatus</i>	4-8
<i>Lissotriton vulgaris meridionalis</i>	Central Italy	W-Switzerland	Released/escaped prior to 1975 by private parties or researchers.	Competition with other <i>Lissotriton</i> newts and potential hybridization with native <i>L. v. vulgaris</i>	This study
<i>Natrix natrix helvetica</i> – S-Lineage	N-Italy or Ticino	W-Switzerland	Escaped in the 1970s from a reptile park	Potential hybridization and competition with native <i>N. n. helvetica</i>	9
<i>Natrix tessellata</i>	Ticino	Switzerland	Introduced in 1925 to Lake Geneva by herpetologists and then relocated to other lakes in the 1950-60s	Competition with <i>N. maura</i>	10-11
<i>Hierophis viridiflavus carbonarius</i>	Ticino	W-Switzerland	Introduced in the 1960s by enthusiasts	Predation on other reptiles, mammals and birds	B. Gentizon, pers. comm.
<i>Podarcis muralis maculiventris</i>	N-Italy	Austria, Germany, Switzerland	Multiple passive (railway cargo) and active (enthusiasts) introductions throughout the 20th century	Genetic pollution, competition and replacement of native <i>P. muralis</i> lineages	12-14
<i>Podarcis muralis nigriventris</i>	Central Italy	Austria, Switzerland	Multiple passive (railway cargo) and active (enthusiasts) introductions throughout the 20th century	Genetic pollution, competition and replacement of native <i>P. muralis</i> lineages	12-14
<i>Podarcis sicula</i>	Central Italy	UK, Germany (extinct), Switzerland	Probably passive introductions by imports throughout the 20th century	Probable competition with indigenous <i>P. muralis</i>	15-18
<i>Emys orbicularis hellenica</i>	N-Italy	W-Switzerland	Introduced in the 1950s by enthusiasts	Genetic introgression with the “native” <i>E. o. orbicularis</i> lineage	19

¹ Dufresnes et al., 2015; ² Dubey et al., 2014; ³ Dufresnes et al., 2017; ⁴ Arntzen, 1999; ⁵ Arntzen and Thorpe, 1999; ⁶ Brede et al., 2000; ⁷ Franzen et al., 2002; ⁸ Dufresnes et al., 2016; ⁹ Dubey et al., 2017; ¹⁰ Mebert, 2011; ¹¹ Dubey et al., 2015; ¹² Schulte, 2008; ¹³ Schulte et al., 2012; ¹⁴ Schulte, Veith and Hochkirch, 2012; ¹⁵ Pascal et al., 2006; ¹⁶ Schulte and Gebhart, 2011; ¹⁷ Hodgkins et al., 2012; ¹⁸ Silva-Rocha et al., 2014; ¹⁹ Raemy, Monney and Ursenbacher, 2013.

A key element to the success of Italian fauna north of the Alps lies in their remarkable ability to colonize the disturbed habitats available in the heavily human-impacted landscapes of Western Europe. These habitats often seem sub-optimal or unsuitable for their native relatives. In crested newts, *T. carnifex* may partly owe its success over *T. cristatus* due to its more generalist habits (Dufresnes et al., 2016). These observations are in line with the century-old idea that more disturbed ecosystems are likely to have more vacant niches that introduced species could inhabit (the “biotic resistance” hypothesis), which however lacks support for terrestrial animals (Jeschke and Genovesi, 2011). Compared to their north-Alpine relatives, Mediterranean taxa naturally inhabit pioneer-like habitats, and may thus be well-adapted to disturbed, recently-shaped sites. More generally, the natural absence of many Italian taxa north of the Alps clearly stems from geographic barriers to dispersal rather than unsuitable ecological conditions. As the *Podarcis muralis* system shows, lineages with narrow realized ecological niches in their native range still became successful invaders under apparently unsuitable conditions, suggesting that their fundamental niches are much broader (Schulte et al., 2012). In Western Europe, environmental conditions may have further improved for Mediterranean aliens over the last century, following global changes in climate (Chown et al., 2014), as illustrated by northwards shifts of distribution (e.g. Lelièvre et al., 2011). Human settlements also provide mild conditions to resist continental environments; for instance, dry microhabitats like railways have favored the establishment of alien reptile populations far north, even if surrounding areas are not necessarily suitable. Moreover, the high genetic diversity of some introduced populations, resulting from multiple origins (e.g. *Podarcis*) or admixed/genetically-rich source populations (e.g. *Lissotriton*) may increase their adaptive potential to new habitats outside their native ranges. Part of this strong diversity may also directly stem from in-situ

crossings by terrarium breeders or laboratory researchers, which often keep distinct lineages as well as artificial hybrids.

Conservation damage and recommendation guidelines

Invasive amphibians and reptiles originating from the Italian Peninsula have numerous direct impacts on Western European taxa, such as predation (one confirmed case), genetic pollution (six confirmed cases) or competition for various resources (all cases), as listed in table 1. Together, they specifically threaten at least ten different local (sub-)species. Moreover, aliens might have potentially contributed to the transmission of pathogens and parasites north of the Alps, although the link has yet to be addressed, and/or is not necessarily obvious in other systems (e.g. Dubey and Shine, 2008). For instance many Italian amphibians are infected but seem tolerant to *Batrachochytrium dendrobatidis* (Bd), the fungus responsible for the devastating disease chytridomycosis (Zampiglia et al., 2013) and now widespread north of the Alps; this includes some of the invaders reported here (e.g. *Pelophylax* and *Triturus*).

Beside these direct conservation impacts, we pinpoint two indirect non-negligible effects. First, the costs associated with the monitoring and eradication of invasive taxa represent a significant budget for wildlife management agencies (Hulme et al., 2008; Keller et al., 2011), which cannot be invested in other conservation programs. Second, these authorities have under some circumstances unintentionally spent resources to protect alien populations, either through global or even specific measures. This is notably the case for invaders morphologically similar to native endangered taxa that can only be discriminated by very few specialists in the field, or by genetic analyses (e.g. *Triturus*, *Pelophylax*, *Hyla*). The expertise of most professional biologists is often limited to the biodiversity naturally found in their region of activity, thus not including closely-related allochthonous

fauna inhabiting neighboring countries. As a result, costly habitat restorations have sometimes favored alien populations (e.g. *Hyla*).

For these different reasons, we recommend performing genetic screening of populations of potential alien origins prior to implementing regional plans like habitat restoration or monitoring. The progresses made in environmental DNA techniques may facilitate and automatize this process in the future (Dejean et al., 2012). Extending the expertise of conservation actors beyond local biodiversity, would also increase the chance to detect alien populations at an early stage. These populations should be eradicated as soon as detected, especially at their margin, in order to preclude further geographic expansions, and therefore minimize the required efforts and costs (e.g. *Podarcis sicula* in the UK; Hodgkins et al., 2012). Even local and apparently non-expanding alien populations may pose a threat in the future: there is often a time lag between introduction of aliens and their spread, from a few years to sometimes several centuries (the “invasion debt”; Essl et al., 2011).

Preventing introductions is generally considered more effective than managing established invaders (Keller et al., 2007). Actions to raise awareness should focus on researchers and captive breeders (responsible for many introductions), together with the general public and authorities unaware of the danger caused by these issues. Herpetological societies are now propagating a more educated attitude towards biological invasions and introduced species, which are relatively new concepts, unconsidered until the last decades. Moreover, enforcing breeding conditions that prevents uncontrolled escapes should be a priority for veterinary services, integrated with the ethical aspects of captive breeding. Given the current worldwide connectivity, the arrival of more exotic species will be inevitable without education, awareness, law enforcement and efficient management programs.

Conclusions

The case of the Mediterranean smooth newts of Italian origin expanding in the outskirts of Geneva supports a common pattern of successful human-mediated introduction of terrestrial vertebrates from the southern to the northern edges of the Alps. In many cases, these releases are the voluntary work of researchers and private parties like wildlife enthusiasts, not passive introductions. Mediterranean aliens may have benefited from the disturbed habitats and the increasingly warm conditions locally found in the heavily impacted landscapes of Western Europe. Their regional expansions are threatening several native species and the difficulty to distinguish them from native relatives without strong expertise and genetic tools have delayed proper management. Lessons should be drawn from these mistakes to prevent future costly invasions.

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