Origin, climate niche, population genetics and intraspecific hybridization of introduced wall lizard populations in Central Europe

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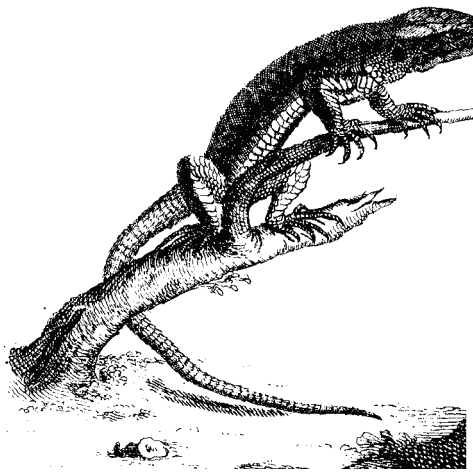

Seps muralis (= *Podarcis muralis*). Aus: Josephi Nicolai Laurenti (1768): Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena. – Wien.

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Chapter	data collecting and processing	data analysis	writing and editing
I	80 %	85 %	80 %
II	60 %	60 %	90 %
III	90 %	100 %	100 %
IV	100 %	80 %	80 %
V	80 %	80 %	70 %
VI	60 %	80 %	90 %
VII	80 %	100 %	90 %

Full Papers (peer reviewed)

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2. **Schulte, U.,** Gassert, F., Geniez, P., Veith, M. & A. Hochkirch (2012): Origin and genetic diversity of an introduced wall lizard population and its non-native cryptic congener. – *Amphibia-Reptilia* 33: 129-140.

3. **Schulte**, **U**., Hochkirch, A., Lötters, S., Rödder, D., Schweiger, S., Weimann, T. & M. Veith (2012): Cryptic niche conservatism among evolutionary lineages of an invasive lizard. – *Global Ecology and Biogeography* 21: 198-211.

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13. **Schulte**, **U**. (2009)*: Expansion einer allochthonen Mauereidechsen-Population bei Leipzig. – *Jahresschrift für Feldherpetologie und Ichthyofaunistik in Sachsen* 11: 2-10.

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19. **Schulte**, **U**., Kwet, A. & A. Nöllert (2011)*: Die Mauereidechse – Reptil des Jahres 2011. – *Reptilia* 90: 60-68.

20. **Schulte**, **U**., Laufer, H., Mayer, W. & A. Meyer (2010)*: Die Mauereidechse – Reptil des Jahres 2011. – *Broschüre zum „Reptil des Jahres 2011*“ der AG Feldherpetologie der Deutschen Gesellschaft für Herpetologie und Terrarienkunde (DGHT), der Österreichischen Gesellschaft für Herpetologie (ÖGH), der Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz (karch) und des Naturschutzbundes Deutschlands (NABU). 32 S.

Contributions to symposia and congresses

1. **Schulte**, **U**., Hochkirch, A. & M. Veith (2012): Invasive Mauereidechsen in Deutschland: Ursprung, Klimanischenbreite, genetische Diversität und Hybridisierung mit heimischen Populationen. – Vortrag auf der Jahrestagung der AG Lacertiden der Deutschen Gesellschaft für Herpetologie und Terrarienkunde, Gersfeld, 23-25.03.2012.

2. **Schulte**, **U**., Hochkirch, A. & M. Veith (2012): Etablierung eingeschleppter Mauereidechsen-Vorkommen unabhängig von ihrer genetischen Konstitution. – Vortrag auf der 23. Jahrestagung der Österreichischen Gesellschaft für Herpetologie, Naturhistorisches Museum Wien, Wien, 20-22.01.2011.

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4. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Hybridisierung zwischen heimischen und eingeschleppten Mauereidechsen am nördlichen Arealrand. – Vortrag auf der Internationalen Fachtagung "Verbreitung, Ökologie und Schutz der Mauereidechse (*Podarcis muralis*)" der DGHT-AG Feldherpetologie und Artenschutz in Zusammenarbeit mit dem NABU-Bundesfachausschuss Feldherpetologie/Ichthyofaunistik, der Akademie für Natur- und Umweltschutz Baden-Württemberg und der Arbeitsgruppe Amphibien-Reptilien Biotop-Schutz (ABS), Offenburg, 19-20 November 2011

5. Heym, A., Deichsel, G., Hochkirch, A., Veith, M. & **U**. **Schulte** (2011): Expansion eingeschleppter Mauereidechsen zu Lasten heimischer Zauneidechsen? – Vortrag auf der Internationalen Fachtagung "Verbreitung, Ökologie und Schutz der Mauereidechse (*Podarcis muralis*)" der DGHT-AG Feldherpetologie und Artenschutz in Zusammenarbeit mit dem NABU-Bundesfachausschuss Feldherpetologie/Ichthyofaunistik, der Akademie für Natur- und Umweltschutz Baden-Württemberg und der Arbeitsgruppe Amphibien-Reptilien Biotop-Schutz (ABS), Offenburg, 19-20 November 2011

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8. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Allochthone Mauereidechsen nördlich der Alpen - ein Überblick. – Vortrag auf der Internationalen Fachtagung "Verbreitung, Ökologie und Schutz der Mauereidechse (*Podarcis muralis*)" der DGHT-AG Feldherpetologie und Artenschutz in Zusammenarbeit mit dem NABU-Bundesfachausschuss Feldherpetologie/Ichthyofaunistik, der Akademie für Natur- und Umweltschutz Baden-Württemberg und der Arbeitsgruppe Amphibien-Reptilien Biotop-Schutz (ABS), Offenburg, 19-20 November 2011

9. Egerer, E. & **U**. **Schulte** (2011): Die Mauereidechse - Reptil des Jahres 2011 mit Präsentation des Videos "Szenen aus dem Leben der Mauereidechse". – Vortrag auf der Internationalen Fachtagung "Verbreitung, Ökologie und Schutz der Mauereidechse (*Podarcis muralis*)" der DGHT-AG Feldherpetologie und Artenschutz in Zusammenarbeit mit dem NABU-Bundesfachausschuss Feldherpetologie/Ichthyofaunistik, der Akademie für Natur- und Umweltschutz Baden-Württemberg und der Arbeitsgruppe Amphibien-Reptilien Biotop-Schutz (ABS), Offenburg, 19-20 November 2011

10. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Rapid genetic assimilation of native wall lizards (*Podarcis muralis*) by extensive introgression of introduced Italian lineages. – Talk at the 104th Annual Meeting of the German Zoological Society (DZG), Saarbrücken, 9th to 12th September 2011.

11. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Hybridization between native and introduced populations of the Common Wall Lizard (*Podarcis muralis*) at its northern range margin. – Talk at the 16th European Congress of Herpetology (SEH) and 47. Deutscher Herpetologentag (DGHT), Luxembourg and Trier, 25th to 29th of September 2011.

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13. Egerer, E. & **U**. **Schulte** (2011): Die Mauereidechse - Reptil des Jahres 2011 mit Präsentation des Videos "Szenen aus dem Leben der Mauereidechse". – Votrtrag auf der DGHT Nachzuchttagung, Trier, 28.09-02.10.2011.

14. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Invasive Mediterranean wall lizards (*Podarcis muralis*) in Central Europe: geographic origin, climatic niche breadth and hybridization with native lineages. – Talk at the Second Mediterranean Congress of Herpetology, topic II: Impact of global changes on the Mediterranean herpetofauna, Marrakech, Morocco, 23-27.05.2011.

15. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Hybridisierung zwischen eingeschleppten Mauereidechsen-Linien und heimischen Populationen in Baden-Württemberg. – Poster auf der Jahrestagung der AG Lacertiden der Deutschen Gesellschaft für Herpetologie und Terrarienkunde, Gersfeld, 8-10.04.2011.

16. **Schulte**, **U**., Hochkirch, A. & M. Veith (2011): Kolonisierung und Hybridisierung eingeschleppter Mauereidechsen in Deutschland. – Vortrag auf der 22. Jahrestagung der Österreichischen Gesellschaft für Herpetologie, Naturhistorisches Museum Wien, Wien, 21-23.01.2011.

17. **Schulte**, **U**., Lötters, S., Veith, M., Hochkirch, A. & D. Rödder (2010): Cryptic niche conservatism among evolutionary lineages of an invasive lizard. – Talk at the 40th Anniversary Meeting of the Gesellschaft für Ökologie (GfÖ), The future of biodiversity, Gießen, August 30th to September 03rd, 2010.

18. **Schulte**, **U**., Hochkirch, A., Lötters, S., Rödder, D., Schweiger, S., Weimann, T. & M. Veith (2010): Cryptic niche conservatism among evolutionary lineages of an invasive lizard. – Vortrag auf der 46. Jahrestagung der Deutschen Gesellschaft für Herpetologie und Terrarienkunde, Frankfurt/M. 2-5.09.2010.

19. **Schulte**, **U**., Hochkirch, A., Lötters, S., Mayer, W., Rödder, D., Schweiger, S. & M. Veith (2010): Intraspezifische Variation im Etablierungserfolg invasiver Mauereidechsen (*Podarcis muralis*) in Mitteleuropa. – Vortrag auf der Tagung Arbeitskreis Biogeographie, Verband der Geographen an Deutschen Hochschulen (VGDH), Trier 7-9.05.2010

20. **Schulte**, **U**. (2010): Eingeschleppte Mauereidechsen in Deutschland – wie wichtig ist die geographische Herkunft für den Etablierungserfolg? – Vortrag auf der Jahrestagung der AG Lacertiden der Deutschen Gesellschaft für Herpetologie und Terrarienkunde, Gersfeld, 12-14.03.2010.

21. **Schulte**, **U**. & B. Thiesmeier (2009): Befragungen in der Feldherpetologie – ein wenig genutztes Instrument. Methoden der Feldherpetologie. – Poster auf der Internationalen Tagung der AG Feldherpetologie der DGHT, des NABU Bundesfachausschusses Feldherpetologie und der Landesgemeinschaft Natur und Umwelt NRW „Methoden der Feldherpetologie“, Bonn, 8-9.11.2008.

GENERAL INTRODUCTION

In autumn 2011 the global human population has reached a new maximum of seven billion people. The increasing mobility of mankind, the expanding international commerce, the ongoing globalization and urbanization worldwide are accelerating the introductions of non-native biota to a formerly unknown extent (Jeschke & Strayer 2005, McKinney 2006, Perrings *et al*. 2010). This fact was already recognized by Charles Elton, the 'founder' of the science of 'Invasion Biology' more than fifty years ago (Elton 1958). Negative effects associated with introduced species have been recognized by a growing number of scientists, including both economists and conservationists. Biological invasions may have severe ecological consequences, such as a loss of native biodiversity or a modification of ecosystem processes. These effects are often associated with enormous costs caused by a reduction of agricultural productivity up to human health concerns (Mack *et al*. 2000). Consequently, the exponential increase in the number and spatial distribution of alien species is recognized as a severe problem in nature conservation (Perrings *et al*. 2005, Strayer *et al*. 2006). Nevertheless, the primary concern of societies about biological invasions arises from species, pathogens and their vectors that have been causing substantial economic harm (Perrings *et al*. 2001). Advances in molecular biology, computational speed and modelling approaches have enhanced the relatively young scientific field of 'Invasion Biology' to expand rapidly to a multifaceted research field (Lockwood *et al*. 2007, Davis 2009). The fields' relevance is highlighted by a steadily increasing number of publications and two leading scientific journals with a clear focus on biological invasions (*Diversity and Distribution*, founded in 1998, and *Biological Invasions,* founded in 2008).

Although there is still a lack of consensus on invasion terminology, introduced species are usually (and throughout this thesis) considered as invasive, once they sustain self-replacing populations over several life cycles and as a consequence of their spread i) alter ecosystem processes, ii) displace native species, iii) introduce pathogens and parasites, or iv) cause economic costs (Colautti & Richardson 2009, Clout & Williams 2009, Catford *et al*. 2011). Biological invasions are usually considered as the final stage of a transitional process, in which the invader continuously progress through a series of stages from transport to introduction, establishment and spread (Kolar & Lodge 2002). Depending on whether we have to deal with unintentional or deliberate introductions, potential invaders have to pass the transport phase under different circumstances and difficulties and begin as propagules in a potential donor region. Provided that propagule pressure, abiotic factors and community interactions aid the transition of the invader to multiple filters (see Fig. 1), it might persist long enough to reproduce in the novel habitat, thus reaching the stage of successful establishment (Colautti & MacIsaac 2004). At the next invasion stage the invader might expand its range (usually after a lag period) and become widespread. Finally, the species might have a significant economic or ecological impact, i.e. reaching the final stage of the invasion. However, most introductions fail and only a small subset of introduced species becomes invasive. The loss of species from invasion stage to

invasion stage is known as the 'Tens Rule' by Williamson (1996), suggesting that only ca. 10% of the species in one invasion stage will reach the next stage (i.e. only 1/10.000 of the transported species will become invasive). However, the 'Tens Rule' is debated controversially (see Williamson & Fitter 1996, Jeschke & Strayer 2005, Lockwood *et al*. 2007). The complexity of ecosystems and the idiosyncratic and unpredictable nature of invasions often hamper the objective assessment of species as 'invasive'. Critical assessments of the ecological effects need to consider any potential impact on native biota, including direct effects of competition, predation, mutualism and hybridization as well as indirect effects through positive interactions with other species or changes in the abiotic environment.

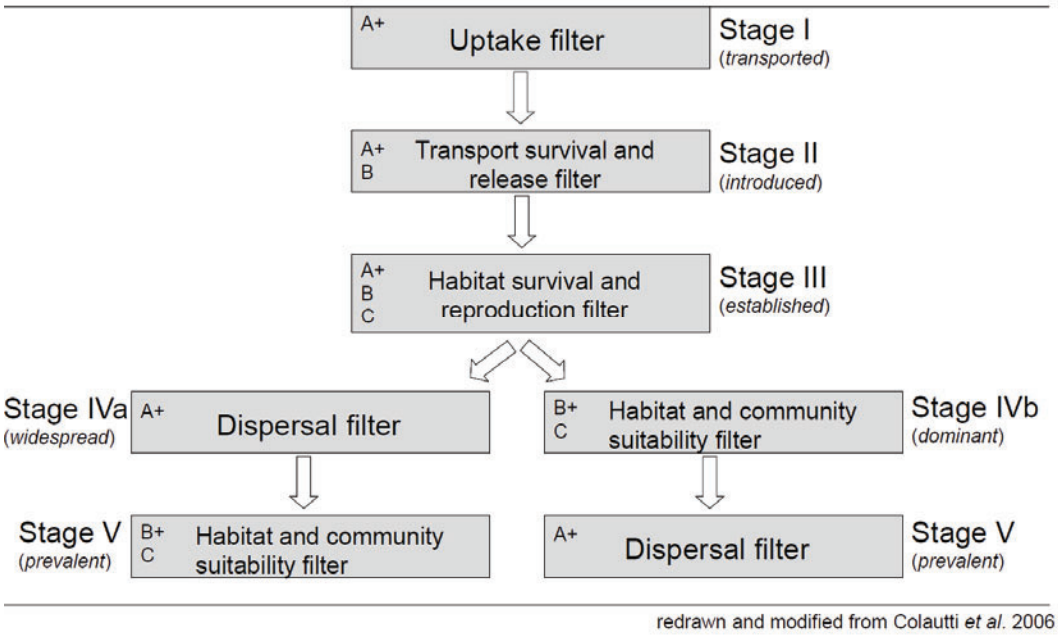

Fig. 1: The series of successive stages within invasion processes. The transition of species to each stage is facilitated (+) or impeded (-) by three classes of determinants: (A) propagule pressure, (B) abiotic factors and (C) community interactions. Filters, such as survival and reproduction act at stages to preclude transition between them and can lead to propagule biases. Note that species can be widespread but rare (stage IVa), localised but dominant (stage IVb) or widespread and dominant (i.e. stage V). Redrawn and modified from Colautti *et al*. (2006).

Prerequisites and determinants of establishment success

Although biological invasions are by far too complex to be predictable, at least some predictions are needed to evaluate competing hypotheses. A considerable amount of research has been carried out to i) determine which mechanisms drive invasions and to ii) evaluate the impact of invasions in order to control and prevent them in the future. The increasing scientific interest in the field of invasion ecology is demonstrated by as many as 29 leading hypotheses in plant invasion ecology, summarized by Catford *et al*. (2009). Depending on the scale (I. macroecological-scale, II. ecosystem-scale, III. species-scale) and invasion stage, several factors that facilitate or inhibit invasion processes have been suggested. While most studies, which aimed to identify traits associated with invasion success focused on intended introductions and the post-establishment stage, only a few focused on the traits favouring stowaways during transport and early invasion stages (see Chapple *et al*. 2012). From a

macroecological perspective, climate matching between the native and introduced range of a species increases the probability of successful invasion (e.g. Bomford *et al*. 2009, Van Wilgen and Richardson 2012, but see Chapter I). Furthermore, many hypotheses attributed invasion success to invader- and ecosystem-characteristics (Catford *et al*. 2009). At this species-ecosystem-level major determinants of invasion success are: i) life history and behavioural traits of the invader (Holway & Suarez 1999, Pyšek & Richardson 2007), ii) resource availability (Lockwood *et al*. 2007, Lohrer *et al*. 2011), and iii) the absence of natural enemies in the introduced range (e.g. Elton 1958, Colautti *et al*. 2004). At the species-level, the genetic architecture of the founding population has also been suggested to be decisive for the success of species introductions (Lee 2002).

Climatic suitability as a prerequisite for establishment

Climatic suitability constitutes the baseline condition for the establishment of species. Due to the existence of high resolution climate models, it is meanwhile also relatively easy to test. Different models have been developed to predict current and future species distributions (species distribution models, SDMs, Guisan & Thuiller 2005). Most of these models use a climate matching approach in order to identify regions, where the establishment and spread of an invader is likely due to a resemblance between the conditions within its native and introduced range (Bomford *et al*. 2009, Rödder & Lötters 2009, Perrings *et al*. 2010). If the climatic conditions of both ranges are highly similar, it is likely that the invader will establish more readily, because of preadaptation (Treier *et al*. 2009). For the interpretation of SDMs most studies assume that niches (realized and fundamental niche) do not change over time and space ('niche conservatism'; e.g. Losos 2008, Revell *et al*. 2008). However, considering the adaptive capabilities and wide distribution of some species there is increasing evidence that niches are variable across time and space (e.g. Peterson & Holt 2003), indicating that niche evolution may particularly be likely among intraspecific evolutionary lineages (Davis 2009, Holt 2009). A promising alternative to purely climate-based models, which represent the common types of SDMs, are population-dynamic and eco-physiological models that take the species physiology, habitat availability, dispersal dynamics and interspecific competition into account independent of current occurrence data (Crozier & Dwyer 2006, Kearney & Porter 2009, Kolbe *et al*. 2010, Gillingham *et al*. 2012).

Beneficial life history traits and habitat characteristics

Beside climatic conditions as prerequisites several other ecological factors are thought to explain establishment success. Due to the high number of potential causal mechanisms during every invasion event, the discipline invasion ecology has been criticized for a lack of general characteristics. Colautti *et al*. (2006) scanned about 1.000 articles focusing on 13 traits associated with invasiveness, but found only few consistencies. Several life history traits of the invader have been associated with invasiveness. Generalist species with broad ecological and physiological tolerance, high genotypic and

phenotypic plasticity (including behavioral flexibility), short life cycles, early sexual maturity, rapid growth-rates and a high fecundity should have advantages in becoming a successful colonizer (Elton 1958, Losos *et al*. 1997, Marchetti *et al*. 2004, Sutherland 2004, Van Wilgen & Richardson 2012). Recently, the importance of inter- and intraspecific variation in behavioral syndromes has been pronounced to influence the success within different invasion stages (Chapple *et al*. 2012). However, invasiveness is closely linked to available resources and thus may change from one environment to another.

While a large body of literature with a focus on invader traits exists, quantifying the invasibility of ecosystems, defined as the vulnerability of a habitat to invasion, has received less attention (Catford *et al*. 2011). This might be caused by the difficulty of examining levels of invasion among ecosystems by using comparable metrics (MacArthur 1970, Sax *et al*. 2007). Recently, Catford *et al*. (2011) recommended two invasion indices: i) relative alien species richness and ii) relative alien species abundance to measure the contribution of introduced species to a community. Taking into account global biogeographic patterns, the invasibility varies between different ecosystem regions. Regions that have never been geographically or ecologically isolated, may be considerably less susceptible for disturbances caused by invasive species than for example isolated island ecosystems with a high degree of endemism (e.g.: Hawaii, Guam; Lowe *et al*. 2000). Nevertheless, homo-genization of biota at large scale can be observed within disturbed urban areas worldwide and it is likely that in these degraded habitats introduced species can benefit from the absence of their native enemies through resource allocation (Enemy-release hypotheses, Keane & Crawley 2002, Colautti *et al*. 2004). As a result, within many bigger city cores introduced generalists are more abundant than native plant species, which get more often restricted to peripheral city areas (McKinney 2006).

Invasion genetics: evolutionary potential and conservation concern

Relatively time saving and meaningful conclusions towards factors that determine post-introduction invasion success can be obtained through analysing the genetic architecture of introduced populations (Colautti *et al*. 2006). There is mounting evidence from studies across a wide range of taxa that a high genetic diversity and attributes like additive genetic variance, epistasis, heterosis, genetic drift and genomic rearrangements promote the success of invaders as they provide the genetic substrate upon which natural selection could act and therefore allow adapting to new environments (reviewed in Lee 2002). The mentioned author suggested that the ability of invasive species to respond to natural selection might be more important for their invasion success than broad physiological tolerance or plasticity. In general, the genetic diversity of the source population, which varies across the range of a species (being usually high in the centre of the species' geographic range and low at the expanding range margins), contributes to the genetic diversity within invasive populations (see Fig. 2).

Propagule pressure, defined as the number of founder individuals (propagule size), the number of source populations (e.g. introduced genotypes) and the frequency of introductions (propagule

number) has been shown to be an important determinant of invasion success (Williamson 1996, Ricciardi *et al*. 2011). Some authors even suggest that propagule pressure is the key driver of invasions (Lockwood *et al*. 2005, Colautti *et al*. 2006, Simberloff 2009). In general, it is thought that a large propagule size enhances establishment probability, while diminishing effects of demographic stochasticity, whereas continual introductions (propagule number) act as a buffer against temporarily unfavourable environmental conditions (Fig. 2, Simberloff 2009).

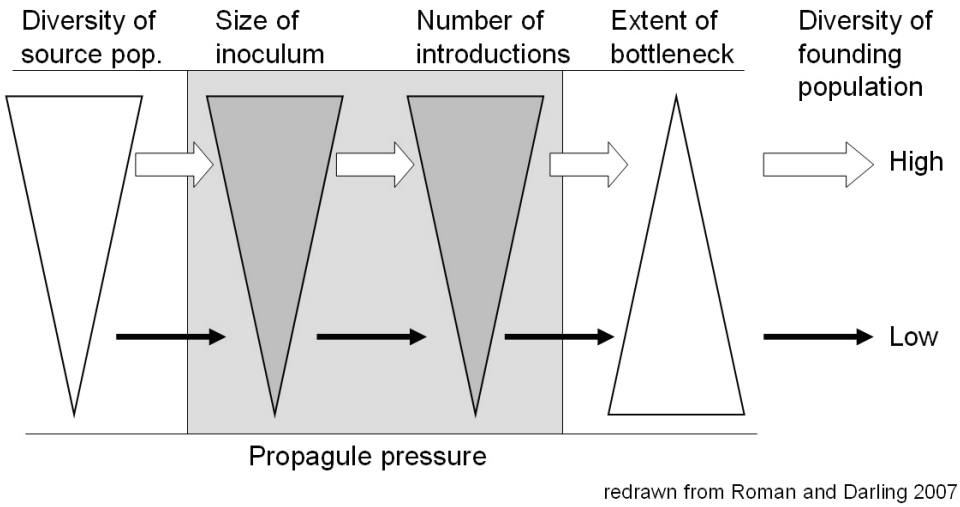

Fig. 2: Important factors contributing to the genetic diversity within invasive populations. The magnitude of each factor is indicated by triangles from high to low from the base to the point (slightly modified from Roman & Darling 2007).

Furthermore, multiple introductions, particularly from a variety of source regions, may increase genetic diversity and therefore the evolutionary potential of the founding population. Furthermore, there is increasing evidence that "multiple introductions of invasive species may be the rule rather than the exception" (Novak *et al*. 2007). A textbook example is the brown anole (*Anolis sagrei*) invasion in Florida, in which admixture of lineages from multiple regions in Cuba increased the genetic diversity of invasive populations and might have enhanced the species' invasiveness (Kolbe *et al*. 2008). Another example is the ladybird *Harmonia axyridis*, one North American invasive population of which was formed by admixture between eastern and western Asian native range populations serving as a 'bridgehead population' for the invasion of other parts of the world (Lombaert *et al*. 2011). As a consequence of creating novel hybrid genotypes the fitness and adaptability to new or changing environments might increase within mixed populations and challenge the control of invasive species (Kolbe *et al*. 2004, Lockwood *et al*. 2005, Verhoeven *et al*. 2011).

From the perspective of species conservation the most devastating consequences of introductions result from predation, competitive exclusion (Vitousek *et al*. 1997, Blackburn *et al*. 2004) and inter- and intraspecific hybridization (see Chapter V). The consequences from hybridization can range from negative fitness effects, such as a loss of regional adaptations to outbreeding depression and the displacement of the native population by gene pool swamping (Allendorf *et al*.

2001, Olden *et al*. 2004, Holsbeek *et al*. 2008, Hochkirch & Lemke 2011, Sacks *et al*. 2011). This is particularly important for the persistence of populations at the range margin, since they may have developed stronger local adaptations in order to cope with episodes of unfavourable environmental conditions. However, some authors challenge homogenization to be a major conservation threat on the long run, since the mixing of species can also promote new radiations and species diversification (e.g. Rosenzweig 2001).

In contrast to those studies that pronounced high propagule pressure and high genetic diversity as requirements or determinants for invasion success, some examples exist where single and severe founder events, resulting in serial bottlenecks and reduced genetic variation, do not appear to be a barrier for successful biological invasions (Simberloff 1989, Tsutsui *et al*. 2000, Zayed *et al*. 2007). For example, the source of the racoon invasion (*Procyon lotor*) in the federal state of Hesse in Germany can be traced back predominantly (beside individuals that escaped from zoos) to the release of only two pairs of the species in 1934 into suitable habitat without natural predators in the Sauerland (Hohmann *et al*. 2001). Similarly, bottlenecks have reduced the genetic diversity of introduced populations of the widespread and harmful invasive Argentine ant (*Linepithema humile*) in California (Tsutsui *et al*. 2000). The species' response to this severe genetic load, relative to native populations, was a reduced intraspecific aggression among nests and a formation of supercolonies resulting in a widespread ecological success. This example illustrates that in some situations behavioural flexibility can compensate low levels of genetic diversity. Irrespective of these different results, the inevitable bias to analyse nearly exclusively successful invasive populations has to be considered (Marchetti *et al*. 2004, Voison *et al*. 2005, Miller & Ruiz 2009). As comparative studies of successful and failed invasions of an introduced species are virtually impossible, the information on the role of the genetic constitution for population extinctions remains unknown.

A very promising approach to understand the genetic processes associated with invasions is the fine scale genetic analysis at the invasion front of expanding populations (Hochkirch & Damerau 2009, Ramakrishnan *et al*. 2010). It is likely that these processes have a large overlap with natural range expansions under climate change scenarios. Surprisingly, there is a lack of studies that have investigated the genetic structuring during range expansion (regardless of native or invasive) at a local scale, although the necessary tools are available (e.g. highly polymorphic nuclear markers, different demographic models of expansion, Estoup *et al*. 2004, Parisod & Bonvin 2008). Those few studies available demonstrated that significant genetic structuring can arise at very small spatial and temporal scales (Herborg *et al*. 2007, Short & Petren 2011). The latter authors showed that during the recent range expansion of the invasive gecko *Hemidactylus mabouia* in Florida more recently colonized sites (~ 1990s) exhibited a higher genetic structuring (at some localities among tens of meters) and lower genetic diversity than earlier colonized sites. In general, these patterns of a decrease in genetic diversity at the expanding range margin represent general patterns, which have also been found during processes of postglacial recolonization (Hewitt 2000, Hampe & Petit 2005, Parisod & Bonvin 2008). It

is thought that genetic diversity is lost during expansion due to smaller population sizes, partial isolation, strong local founder effects, genetic drift and higher selection pressure (Hewitt 2001). In contrast to the central-margin hypothesis, a clustered distribution of high regional diversity within peripheral populations has been shown, which resulted from historical admixture processes (Petit *et al*. 2003, Eckert *et al*. 2008). Among all genetic processes acting on the leading edge of populations, the founder effect is assumed to be the key driver for a reduction of genetic diversity and an increase of differentiation. However, studies on small founder populations of salmonids (*Thymallus thymallus*) and invasive reed canary grass (*Phalaris arundinacea*) suggest that directed natural selection can act even stronger than random drift in the diversification of peripheral populations, contrary to classical evolutionary theories (Wright 1931, Koskinen *et al*. 2002, Lavergne & Molofsky 2007). Beside genetic processes, behavioural and life history traits of a colonizing species which shape its dispersal mode as well as landscape patterns contribute to the genetic structure during range expansions (Wilson et al. 2009). Finally, human assisted jump-dispersal (particularly in urban areas) and the admixture of different founder individuals might explain the genetic structure of populations (Kolbe *et al*. 2008, Chapple *et al*. 2012).

The need for a conceptual framework

It is obvious that in most invasion scenarios anthropogenic modified interactions of propagule pressure, abiotic and biotic characteristics (see Fig. 1, Catford *et al*. 2009) drive the invasion process. In this context, the concept of invasion pressure (*IP*) has been developed by Gilpin (1990), which quantifies the probability that an environment will experience an invasion within a certain time period (Davis 2009). Invasion pressure is defined as an interaction of three variables: invader traits, the invasibility of the environment and propagule pressure (Gilpin 1990).

Species introductions are always idiosyncratic cases for which the outcome is difficult or even impossible to predict due to the complexity and multitude of interactions during invasion processes. Therefore, generalization should be treated with caution. On the other hand, one can find multiple species invasion studies aiming to identify generalities within macroecological approaches (e. g. Blackburn & Duncan 2001). While in depth analyses of a single species might miss generalities, oversimplification in search of predictability might also be problematic. Catford *et al*. (2009) provide a theoretical framework to integrate different invasion hypotheses and criticise that most individual invasion case studies have led to a fragmentation in the field 'Invasion Biology'. These authors and other scientists (Sax *et al*. 2005, Davis 2009) suggest a greater exchange between the field and the disciplines of succession and community ecology (Chesson 2000), landscape ecology (With 2002) and conservation biology (Lockwood *et al*., 2005) as well as sociology and philosophy. An encouraging basis for synthetic studies is Wilson's concept of a 'taxon cycle' (Wilson 1959, 1961), which pronounces attributes that historically, formed phases of expansion and contraction of native

populations. This knowledge of the taxon cycle of a species can provide valuable information to interpret the success or failure of introductions of this species (Ricklefs 2005). As patterns of native and non-native colonization processes are rather similar, there is a great potential of theoretical synergy among these disciplines.

*Introductions of the Common Wall Lizard (***Podarcis muralis***) as a study system*

The large number of introduced wall lizard populations in Central Europe, the UK and parts of North America represent an excellent model system for the study of different ecological and evolutionary processes of species invasions. A first survey on the extent of introduced wall lizard populations in 2007/2008 revealed a surprisingly high number of non-native populations in Germany (74 populations until June 2008, Schulte *et al*. 2008, Schulte & Thiesmeier 2009), considering that the species had never been documented as an invasive species or paraneozoon in Germany before (Geiter *et al*. 2001). While the oldest introductions of wall lizards in Germany date back to the 1870s (Dürigen 1897), a large part of populations emerged in the 21st century (Fig. 3a). About three quarters of populations originated from intended introductions mostly into suitable habitats, while one quarter is thought to stem from stowaways along railway stations (Fig. 3b). Meanwhile, the number of documented wall lizard introductions steadily increased to 84 populations (see Chapter VII as of 25th of August 2011). The origin of most introduced populations was unknown, but those with existing data on the source area stem from different regions in the Mediterranean (Dürigen 1897, Schulte 2008).

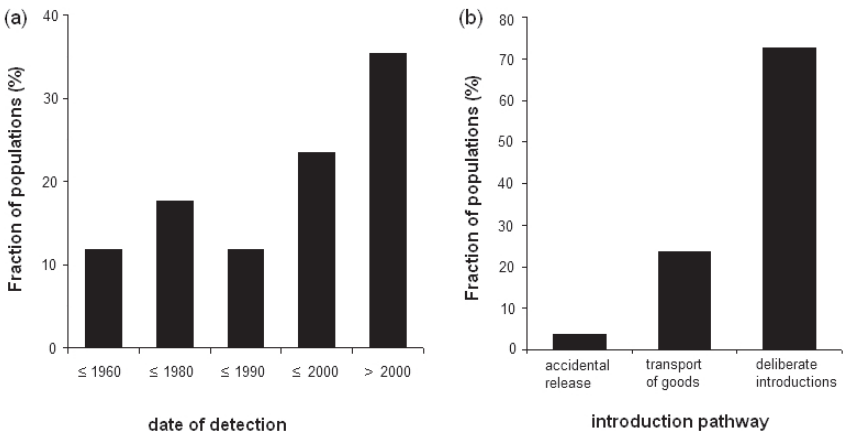

Fig.3: (a) Date of first detection of introduced wall lizard populations in Germany (n = 51); (b) Presumed or known pathways of wall lizard introductions in Germany (n = 68).

Due to the clear phylogenetic structure within its native range and the very different invasion histories of invasive populations (donor region, time of introduction, propagule pressure), the wall lizard invasion provides an excellent model system for studying intraspecific variation in establishment success of an invasive species. Furthermore, reports of introduced populations at the northern range margin of the species (urban areas of Upper Rhine Rift) offered the possibility to study intraspecific hybridization and introgression of alien lineages in mixed populations.

Structure of this thesis

In this PhD thesis determinants of the invasion success of introduced wall lizards in Central Europe, as well as the genetic consequences of introductions and intraspecific hybridization between native and introduced lineages of *P. muralis* have been studied. The primary aim was to determine the main factors responsible for the invasion success of the species and its different evolutionary lineages in order to obtain a differentiated view on its invasive potential and to achieve sufficient knowledge for a realistic risk assessment. I performed a 'top-down approach', aiming to identify the baseline-factors first, and subsequently narrowing the perspective towards potential causal mechanisms and evolutionary processes (Catford *et al*. 2009). Based upon an assignment of the geographic origin of 77 populations, I tested the hypothesis of climate matching and intraspecific variation in climatic niche breath. Subsequently I focused on the genetic composition of populations with different invasion history. Finally, I studied the extent and pattern of intraspecific hybridization between introduced and native populations in south-western Germany as well as the impact of introduced wall lizards on native sand lizards (data not shown) to evaluate the invasiveness of the species.

In **Chapter I**, I aimed at identification of the role of the source region of introduced wall lizards in Central Europe as a determinant of their invasion potential. To test hypotheses associated with biological invasions it is crucial to accurately identify the geographic origin of the invader (Lombaert *et al*. 2011). Through the cooperation with Werner Mayer and Silke Schweiger (Naturhistorisches Museum Wien), I was able to access a well-structured phylogenetic data set of my model species. Hence, I could test whether evolutionary lineages of the wall lizard vary in their climate niches and invasive potential. Furthermore, I tested whether lineage-specific models show a better performance than combined models. Using DNA-barcoding, all currently known introduced wall lizard populations in Germany and some additional populations in Switzerland, Liechtenstein and Austria (N = 77) were assigned to their geographic origin (in cooperation with the Naturhistorisches Museum Wien). The resulting dataset was used in combination with species distribution models (SDMs) based on climatic information at native and invasive ranges to test for intra-specific niche divergence among mitochondrial DNA (mtDNA) clades of *Podarcis muralis*. Niche similarity among lineages was assessed and the predictive power of a combination of clade-specific SDMs was compared with a combined SDM using the pooled records of all lineages. This was the first approach to test for differences or similarities among climatic niches at the intraspecific level (different evolutionary lineages of *P. muralis*) in biological invasions. The results have been published in *Global Ecology and Biogeography* 21: 198-211 (2012).

A large number of individuals (> 800) had to be genotyped for the population genetic studies. Since tail-clipping harms the specimens in their locomotory performance and energy reserves, I tested the use of buccal swabs as non-invasive sampling method for microsatellite analysis. **Chapter II** summarizes the comparison of both sampling methods for genotyping and has been published in *North-Western Journal of Zoology* 7: 325-328 (2011).

Chapter III and **IV** aim to identify the geographic origin of two other *Podarcis* species in Central Europe: *Podarcis siculus* and *Podarcis liolepis*. In Chapter III the source region of the only known *P. siculus* population north of the Alps could be assigned, while Chapter IV comprises the first record of *P. liolepis* introduced in Germany within a syntopic population of its congener *P. muralis*. Using DNA-barcoding and microsatellites, I identified the geographic origin of both introduced species, tested for hybridization between them and compared levels of genetic diversity between native populations from southern France and introduced populations in Germany. The two chapters have been published in *Herpetozoa* 24: 96-97 (2011) and *Amphibia-Reptilia* 33: 129-140 (2012).

While the majority of invasive populations is found outside the native range of *P. muralis*, some introduced populations also exist at the northern range margin in south-western Germany. Within **Chapter V** I assessed the extent of intraspecific hybridization in mixed populations within contact zones of alien and native lineages. For this purpose I first used an mtDNA marker (cyt*b*) to infer the geographic origin of introduced lineages in purebred introduced populations and their frequency in mixed populations. Accordingly, I analyzed the degree of differentiation among and within populations with different invasion histories (using 13 microsatellite loci), including the detection of recent hybridization events. Finally, I tested the hypothesis that the genetic diversity of introduced populations depends on the degree of admixture and on their source region. The results of this study provide the first direct evidence for the invasiveness of introduced wall lizards, and therefore suggest defining evolutionary lineages of *P. muralis* as 'invasive', although this species is native to south-western Germany. This article is in press in the journal *Molecular Ecology*, doi: 10.1111/j.1365-294X.2012.05693.x.

When studying the population genetics of an invasive species the invader has been rarely sampled across its colonized range, in order to detect genetic structuring and routes of dispersal (Short and Petren 2011). **Chapter VI** includes a fine scale analysis of the genetic structure that aroused during the range expansion of a thriving wall lizard population in Passau. I reconstructed the invasion history of this large population in order to i) analyze the genetic structure across localities that have been colonized at different times, to ii) test for a loss of genetic diversity and bottlenecks at more recently colonized locations and to iii) estimate the speed of expansion within this invasion event. Available benchmark data of this population allowed me to retrospectively validate my results.

The final **Chapter VII** summarizes important information for field herpetologists and conservationists. Data on the distribution, habitat, presumed or known sources and pathways, ages, estimated population sizes as well as on the geographic origin of all known introduced wall lizard populations ($N = 82$) in Germany until 25th of August 2011 are presented (published in *Zeitschrift für Feldherpetologie* 18: 161-180 (2011)). Furthermore, I address the phenotypic assignment of populations to evolutionary lineages and discuss the problem of how to deal with invasive populations in the light of the current conservation legislation.

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CHAPTER I

Cryptic niche conservatism among evolutionary lineages of an invasive lizard

Schulte, U., Hochkirch, A., Lötters, S., Rödder, D., Schweiger, S., Weimann, T. & M. Veith (2011): Cryptic niche conservatism among evolutionary lineages of an invasive lizard. – *Global Ecology and Biogeography* 21: 198-211.

Abstract

Aim There is increasing evidence that the quality and breadth of ecological niches vary among individuals, populations, evolutionary lineages and therefore, also across the range of a species. Sufficient knowledge about niche divergence among clades might thus be crucial for predicting the invasion potential of species. We tested for the first time whether evolutionary lineages of an invasive species vary in their climate niches and invasive potential. Furthermore, we tested if lineage-specific models show a better performance than combined models.

Location Europe.

Methods We used species distribution models (SDMs) based on climatic information at native and invasive ranges to test for intra-specific niche divergence among mitochondrial DNA (mtDNA) clades of the invasive wall lizard *Podarcis muralis*. Using DNA barcoding, we assigned 77 invasive populations in Central Europe to eight geographically distinct evolutionary lineages. Niche similarity among lineages was assessed and the predictive power of a combination of clade-specific SDMs was compared with a combined SDM using the pooled records of all lineages.

Results We recorded eight different invasive mtDNA clades in Central Europe. The analyzed clades had rather similar realized niches in their native and invasive ranges, whereas inter-clade niche differentiation was comparatively strong. However, we found only a weak correlation between geographic origin (i.e. mtDNA clade) and invasive occurrences. Clades with narrow realized niches still became successful invaders far outside their native range, most probably due to broader fundamental niches. The combined model using data of all invasive lineages achieved a much better prediction of the invasive potential.

Conclusions Our results indicate that the observed niche differentiation among evolutionary lineages is mainly driven by niche realization and not by differences in the fundamental niches. Such cryptic niche conservatism might hamper the success of clade-specific niche modelling. Cryptic niche conservatism may in general explain the invasion success of species in areas with apparently unsuitable climate.

Key words Europe, invasion success, mtDNA, niche conservatism, niche evolution, *Podarcis muralis,* species distribution model.

Introduction

Globalization has dramatically accelerated the introduction of alien species (Perrings *et al*. 2005). The threat to biota posed by invasive species has been identified as one of the most severe problems in nature conservation (Strayer *et al*. 2006). In addition to negative consequences for species richness and ecosystem function, invasive species can have severe economic impacts (Primentel *et al*. 2000). There is a large body of literature focusing on the identification of common patterns that facilitate invasion processes. Generally, it is thought that climate matching of the novel area to the climate of the native range is a prerequisite for establishment success (e.g. Bomford *et al*. 2009). Other key factors considered as highly correlated with establishment success are propagule pressure (e.g. Simberloff 2009), pre-adaptation (e.g. Treier *et al*. 2009) and escape from natural enemies in the introduced range (e.g. Colautti *et al*. 2004).

Species distribution models (SDMs) are useful tools for identifying climatically suitable regions for possible establishment and hence for predicting the potential invasive range of species (e.g. Peterson and Vieglais 2001, Jeschke and Strayer 2008; Gallien *et al*. 2010, Rödder and Lötters 2010). When interpreting the potential distribution of invasive species in new regions derived from SDMs, it is important to distinguish between a species' fundamental and realized niche. The realized niche is a fraction of the fundamental niche considering physical dispersal limitations and biotic interactions (Hutchinson 1957, Soberón 2007, Godsoe 2010). Up to now, most studies have assumed that niches are constant across the geographical range of a species and some even suggest niche conservatism above species level (e.g. Losos 2008, Revell *et al*. 2008, Hof *et al*. 2010). However, there is increasing evidence that niches may be variable among individuals, populations and consequently across the geographic ranges of species (e.g. Peterson and Holt 2003). Niche evolution may particularly be likely among intraspecific evolutionary lineages (Holt 2009).

Detailed knowledge on fundamental niche divergence among clades might thus be crucial to correctly predict the invasive potential of different intraspecific lineages. Such a lineage-specific modelling approach might provide a more differentiated risk assessment. However, for this kind of modelling an integration of phylogenetic information, distribution data for each lineage and environmental data is inevitably needed. Up to now, these integrative approaches have been restricted to the species level and above (e.g. Warren *et al*. 2008). Studies on the invasion potential of different evolutionary lineages within invasive species are still missing.

Among reptiles, lizards spread via pet trade or cargo and nursery pathways are suggested to exhibit a high establishment success (e.g. Kraus 2009, Rödder and Lötters 2009). Nevertheless, only few non-native reptile species have successfully colonized Europe (Kraus 2009), most of which are found in the Mediterranean (e.g. Carranza and Arnold 2006, Ficetola *et al*. 2009). The wall lizard, *Podarcis muralis*, represents an exception, as it has colonized regions in north-western Europe far outside its sub-Mediterranean native range. Anthropogenic introductions of wall lizards into north-western Europe date back to the 1870s and were mainly seen as a form of environmental enhancement

(Dürigen 1897). Nowadays, about 140 non-native *P. muralis* populations are documented from north-western Europe and in additional, some are known from the New World (Schulte 2008, Burke and Deichsel 2009; Fig. 1A/B). The ecological impact of introduced wall lizards on native communities in north-western Europe is little studied. However, there are cases in which a competitive displacement of the native Sand Lizard (*Lacerta agilis*) and the Common Lizard (*Zootoca vivipara*) has been reported (Schulte *et al*. 2008). In addition, it has been assumed that, at the edge of their range, native wall lizards may be genetically swamped by introduced alien lineages (Schulte *et al*. 2008). Therefore, invasive wall lizard populations may threaten the native local fauna. The origin of most alien populations is unknown (Schulte 2008), but those with existing history stem from different regions in the Mediterranean. Hence, it is of particular interest whether differences of establishment and invasion probability do exist among *P. muralis* of different geographic origin, i.e. of different phylogenetic lineages. Since there is reason to assume that such lineages have evolved adaptations to local environmental conditions (e.g. Holt 2009), we hypothesize that the potential distribution and the invasive occurrence of phylogenetically distinct wall lizard clades are linked to the climates at their native occurrences.

For the first time, we present here a combined mitochondrial DNA (mtDNA) barcoding and SDM approach in order to test the hypothesis that intra-specific niche variation may influence the invasive occurrence of a species. Furthermore, we test if such lineage-specific models show a better performance than combined models. The goals of the present study are (1) to identify the origin of invasive wall lizard populations in Central Europe using mtDNA barcoding, (2) to test if different evolutionary lineages as identified by mtDNA sequences differ in their realized climate niches and in their potential for invasion, and (3) to test if the combination of SDMs developed for each lineage has a better predictive power than a combined SDM using the pooled records of all lineages.

Methods

Study species

Podarcis muralis is a small heliothermic, synanthropic and saxicolous lacertid species, which is widely distributed throughout southern and western Europe. Within its native range the species shows a clear phylogeographic structure (Giovannotti *et al*. 2010; S. S. *et al*., unpublished data). The Western France Clade is confined to the Atlantic part of France and parts of the Pyrenees (see Fig. 1A). The northernmost genetic clade, the Eastern France Clade, is distributed across the south-eastern and eastern parts of France, western Switzerland and western Germany up to Maastricht in the Netherlands. Eastwards the Southern Alps Clade occurs in north-western Italy, the southern Alps and the Inn valley. The Venetian Clade can be found in southern-most Slovenia, north-western Croatia, and the eastern part of the Po plain. In Tuscany, Latium and parts of the Campania, a green-backed and morphologically clearly separated clade (Tuscany Clade) is known (Giovannotti *et al*. 2010). The

Romagna Clade is situated within the northeastern-most Apennine region, whereas the Marche Clade is distributed within Central Italy and western Istria. The Central Balkan Clade occurs on the Balkan Peninsula, in Hungary, Slovakia as well as, in an isolated area in north-eastern Austria (S. S. *et al*., unpublished data; Fig 1B).

Invasive populations and sampling

To obtain information on the distribution of non-native populations, we posted e-mail messages on the major Central European herpetology mailing list (amphibienschutz.de, 1070 subscribers) during autumn and winter 2007/2008. We particularly focused on Germany, where the majority of successful introductions have been reported. In addition, we compiled localities of *P. muralis* introductions from the literature and unpublished reports (Schulte *et al*. 2008 and Appendix S2). We only considered non-native populations in which reproduction was confirmed and a minimum of ten adults has been observed.

In total, 184 lizards (one to ten individuals per population) were captured by hand or by noosing within 77 alien populations of *P. muralis* in Germany (n = 61), Austria (6), Liechtenstein (1) and Switzerland (9). Lizards autotomized the tip of their tail after exerting pressure and were immediately released afterwards. The tail tip was stored in 99.8% ethanol p.a. We also included information from four additional populations from Germany as well as one from the Netherlands, Liechtenstein, Great Britain and Croatia for which reliable information on their origin was available (Appendix S7).

Genetic analysis

We extracted genomic DNA from muscle tissue using the Qiagen DNEasy Blood and Tissue Kit (Qiagen, Hilden) following the manufacturers' protocol. In a preliminary study, 24 populations had already been sequenced for a 887 base pair (bp) fragment of the mitochondrial cytochrome *b* gene (cyt *b*) (Schulte *et al*. 2008). Additionally we sequenced 25 populations for this fragment. For the remaining 28 populations, we sequenced a 656 bp fragment using the primers LGlulk (5'-AACCGCCTGTTGTCTTCAACTA-3') and HPod (3'-GGTGGAATGGGATTTTGTCTG-5') (Deichsel and Schweiger 2004, Podnar *et al*. 2007). Sequencing was performed with the DYEnamic ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich) for sequencing reactions run on a MegaBACE 1000 automated sequencer (GE Healthcare). DNA sequences were corrected and aligned by eye. We did not include ambiguous data from the beginnings and ends of the fragments in the analyses. Sequences were deposited in GenBank under the accession numbers HQ652874-HQ652973. For lineage identification, sequences of invasive populations were aligned to sequences from individuals sampled across the entire native range of *P. muralis* (FJ867389-FJ867394, Giovannotti *et al*. 2010; S. S. *et al*., unpublished data) and *P. liolepis* (AF469436, AF469442, DQ081144; Harris & Sá-Sousa 2002) and fitted into a phylogenetic tree using *P. siculus* and *P.*

melisellensis as outgroups (HQ154646, AY185097, Podnar *et al*. 2004, Appendix S8). We used Bayesian inference to infer the phylogeny as implemented in MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003), applying the parameters of the substitution model suggested by MrModeltest 2.2 (Nylander 2004). We ran the Monte Carlo Markov chain for one million generations, sampling every 100 generations. We discarded 2500 trees as burn-in after checking for stationary and convergence of the chains. Support of the nodes was assessed with the posterior probabilities of reconstructed clades as estimated in MrBayes (Ronquist & Huelsenbeck, 2003). This barcoding approach allowed us to unambiguously assign invasive haplotypes to intraspecific evolutionary *P. muralis* lineages and their respective distribution areas.

Species native occurrence data

To achieve a reliable delineation of the native range of each genetic clade through SDMs, we used 95 unique records (latitude/longitude) of haplotype groups obtained through an extensive sampling for a phylogeographic analysis (Giovannotti *et al*. 2010; S. S. *et al*., unpublished data). The genetic analysis revealed 22 genetic clades of *P. muralis* with unique haplotype groups and well confined ranges, eight of which were found in our invasive samples. We excluded the Romagna and Marche Clades due to limited availability of native and invasive species records and focused on the six remaining clades in our modelling approach. For an estimation of the native range of each clade, we constructed a Minimum Convex Polygon (MCP) considering only samples that were used in the phylogeographic analysis (n = 95). We incorporated 884 additional records in our SDM that fell into one of these MCPs (Fig. 1A/B), 206 species records of which were compiled through literature screening and personal communications (see Appendix S1). The remaining 678 records were obtained from the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN) database on Natura 2000 sites; these were only considered for modelling when their spatial accuracy was lower than 1 km^2. Overall, we compiled 266 records of the Eastern France Clade, 107 records of the Western France Clade, 402 records of the Southern Alps Clade, 82 records of the Venetian Clade, 55 records for the Tuscany Clade, and 149 records for the Central Balkan Clade. When necessary, the BioGeoMancer (http://bg.berkeley.edu/latest; accessed December 2009 to January 2010) and the Alexandria Digital Library Gazetteer Server Client (http://www.middleware.alexandria.ucsb.edu /client/gaz/adl/index.jsp; accessed December 2009 to January 2010) were used for geo-referencing.

SDM predictor selection

For climate data, we used monthly climate layers available through the WorldClim database version 1.4, which is based on weather conditions recorded from 1950-2000 with a spatial resolution of approximately 900 m x 900 m throughout Central Europe (Hijmans *et al*. 2005). Available climate data include monthly mean minimum and maximum temperatures and monthly mean precipitation. Of these, we calculated so called 'bioclim' variables with DIVAGIS 5.4 (http://www.divagis.org; downloaded April 2009; Hijmans *et al*. 2005). We selected variables that are suitable as predictors of the wall lizard's potential distribution based on the species' ecology and life history traits, which should significantly improve the reliability of SDMs (Rödder *et al*. 2010). The final variable set comprised (i) mean temperature of the warmest quarter representing a good predictor for reproduction success as incubation temperature strongly influences hatching time as well as hatchling condition (Van Damme *et al*. 1992); (ii) mean temperature of the coldest quarter which is important for the lizard to display partial winter activity; (iii) minimum temperature of the coldest month, a predictor for successful partial hibernation; (iv) precipitation of the warmest quarter, a predictor for the species' occurrence in its Mediterranean distributional range due to its strong preference for humidity in certain areas (Capula *et al*. 1993). In addition, we included (v) annual aridity and (vi) annual Potential Evapo-Transpiration (PET) derived from the Worldclim data by Trabucco and Zomer (2009). Both variables are not correlated with other variables and are especially important for microhabitat-specific distribution (avoidance of xeric habitats) of the species in its southern range (e.g. Capula *et al*. 1993, Martín-Vallejo *et al*. 1995).

Species distribution models

For SDM computation Maxent 3.3.0 (Phillips *et al*. 2004, 2006; http://www.cs.princeton.edu/~shapire /Maxent; downloaded 15 April 2009) was used, which is a machine learning algorithm for SDM generation derived from environmental (e.g. bioclim) predictors. It yields largely better results than other presence-only/presence-pseudoabsence SDM methods (Elith *et al*. 2006, Heikkinen *et al*. 2006). Maxent performs well even when the number of species point records available for modelling is small (e.g. Hernandez *et al*. 2006, Wisz *et al*. 2008). This approach processes randomly chosen background points as a contrast to the actual records of the species under study during model building. Definition of an area for appropriate background selection is crucial for successful modelling and should reflect the areas potentially accessible to the target species (Phillips 2008). Background points used herein were randomly chosen within the native and invasive areas enclosed by a MCP for each clade (see above and Fig. 1A/B). Maxent allows for model testing by calculation of the Area Under the ROC (Receiver Operation Characteristic) Curve (AUC), based on training and test data, which represent the ability of the model to distinguish presence data from background data (Phillips *et al*. 2006). Furthermore, we tested for the explanative power of each predictor using a jackknife approach, i.e. in Maxent SDMs each predictor was sequentially omitted or, in a second approach, used as single

variable and corresponding AUC values were assessed. We compared the predictive power of a combination of SDMs developed for each lineage to a SDM developed with all records of all clades pooled by computing overlaps in terms of Schoener's D (see below) and a simple linear regression. In the former approach, we combined the potential distributions of each lineage by computing the maximum prediction per grid cell.

Depending on the settings and data types used for model computation, the resulting maps may characterize a species' realized or potential distribution (Elith and Leathwick 2009). This may have severe implications for the interpretation of results. Inclusion of biotic or accessibility predictors may allow an approximation of a species' realized niche, wherein using only presence data and restricting the predictors to environmental variables as we did may rather represent the species' fundamental niche (Peterson 2006, Soberón 2007).

Spatial statistical analyses

In order to visualize the overall levels of divergence in climate niche space, we conducted Principal Components Analysis (PCA) in XLStat 2010 comprising all clades and based on climate conditions extracted at native and invasive occurrences (Fig. 1). To test for niche overlap, similarity and equivalency (for definitions see below), we compared potential distributions between all six native clades and crosswise between native and invasive ranges of three clades with strong invasive occurrence (Southern Alps, Eastern France and Venetian Clade). Within our modelling approach, invasive occurrences of each lineage occurring in populations with more than one origin were treated separately. In the past, niche conservatism was tested using different hypotheses. For example, Graham *et al*. (2004) tested for niche equivalency by asking whether niches of two species are effectively indistinguishable, whereas Peterson *et al*. (1999) tested for niche similarity by assessing whether the niche of one species holds more information about the niche of its sister taxa than expected at random. To test for these hypotheses, we used spatial statistics as proposed by Warren *et al*. (2008) and modified by Rödder and Lötters (2009). As niche overlap index, we used Schoener's *D* (Schoener 1968), which quantifies common parts of two probability distributions as suggested by SDMs trained with native records (X) and invasive records (Y). *D* values range from 0 (no overlap) to 1 (identical SDMs). Significance of results was evaluated with null models testing for niche similarity and equivalency (see below).

For niche equivalency, we applied a randomization test as proposed by Warren *et al*. (2008) that relies on the metric *D*. To compare climate niches of two clades or native and invasive records belonging to one clade (i.e. Eastern France Clade native = 266 vs. Eastern France Clade invasive = 33; Southern Alps Clade native = 402 vs. Southern Alps Clade invasive = 32; Venetian Clade native = 82 vs. Venetian Clade invasive = 21), we created 100 pseudoreplicates by randomly partitioning the pooled sets of occurrence records of both test groups into sets of the same sizes. Subsequently, SDMs were created from each pseudoreplicate and compared using D. The observed values were compared to

the percentiles of these null distributions in a one-tailed test assessing the significance of niche identity. The test assesses niche conservatism in a strict sense, i.e. the effective equivalency of the climatic niche in the native and invasive range of a certain clade. It is expected to be only met if native and invasive populations of one clade exactly tolerate the same climatic conditions and have the same set of environmental conditions available to them (Warren *et al*. 2008).

In order to assess niche similarity, we again used a randomization test of Warren *et al*. (2008). This test compares the similarity of SDMs based on native records in terms of *D* values to the distribution of similarities obtained by comparing them to an SDM obtained by randomly choosing n_{inv} cells from among the cells in the study area of the invasive records. The same procedure was performed in both directions (invasive <> native records) 100 times each for two groups to construct an expected distribution of *D* values between an SDM generated using actual occurrences and one generated from random background data points. Appropriate selection of background points is important, since they can influence the significance of the test. Therefore, we restricted background points to the area defined within a minimum convex polygon comprising all native (likewise invasive) records of each genetic clade (see Fig. 1A/B). These null distributions served as two-tailed test to assess the following null hypothesis: measured niche overlap between native and invasive ranges is explained by regional similarities or differences in available habitat. This hypothesis is rejected if the actual similarity falls outside the 95 % confidence limits of the null distribution. Significantly higher values suggest that SDMs are more similar than expected by chance and lower values indicate greater differences. The distance between the observed overlap value and the closest overlap value in the null distribution can be used as a quantitative measure of distinctness (Rödder and Lötters 2009). Computations of *D*, niche similarity and equivalency were performed with a Perl script (Software ENMTOOLS; http://www.enmtools.com/; downloaded June 2009) developed by Warren *et al*. (2008).

Results

Geographic origin of invasive *P. muralis* populations

Based upon cyt *b* haplotypes, we found eight geographically distinct mtDNA clades (following S. S. *et al*., unpublished data) in 77 invasive populations in Central Europe (Fig. 1A/B; Appendix S7). Posterior probabilities of the clades were high (100) and only some internodes had a lower support (Appendix S8). Combined with reliable information on the origin of eight further populations the two most common haplotypes belonged to the Eastern France Clade (38.8 %; 33/85 populations) and the Southern Alps Clade (37.6 %; 32/85 populations). Invasive populations of the Eastern France Clade were mainly detected in western Germany, particularly in the Ruhr river basin (Fig. 1A). Three of these alien populations belong to the Languedoc Subclade within the Eastern France Clade (3.5 %; 3/85 populations). Populations belonging to the Southern Alps Clade occurred widespread outside their native range up to northern and eastern parts of Germany. The next frequent clade was the

Venetian Clade (24.7 %; 21/85 populations). The Tuscany Clade was found less frequently (mainly in southern Germany, 5.9 %; 5/85 populations). The Western France Clade (3.5 %; 3/85 populations) was found in Rhineland-Palatine and southern Lower Saxony, while the Central Balkan Clade (3.5 %; 3/85 populations) occurred in eastern Germany (Fig. 1A/B). At few localities we found the Marche and Romagna Clades (from Italy)**.** In 19 introduced populations we found haplotypes from more than one source area. Most frequently we determined combinations of the Southern Alps Clade and the Venetian Clade (see Appendix S7). In one population belonging to the Western France Clade we even discovered a haplotype belonging to a different species, *Podarcis liolepis* of the *P. hispanicus* species complex (Renoult *et al*. 2010).

Niche overlap among native clades

On the first two axes of the PCA, all native clades showed a separation in their multidimensional niche space (Fig 1C/D, correlation circle; for eigenvalues and eigenvectors see Appendix S7). Pairwise niche overlap derived from SDMs based on the combination of the six variables ranged from 0.08-0.52 using Schoener´s *D* (Table 1). The highest niche overlap among native clades was found between the Eastern France and Southern Alps Clades ($D = 0.52$), whereas niche overlap of the Central Balkan and Tuscany Clades was much lower ($D = 0.08$). The hypothesis of niche equivalency was rejected in all cases (Table 1). *D*-values of background tests of overlap between $clade_x$ vs $clade_{y\ background}$ were significantly more similar than expected by chance in one case (Cbalk vs $Tusc_{background}$) and significantly more different than expected by chance in two cases (Tusc vs $Ven_{background}$, Tusc vs $Wfra_{background}$). *D*-values of background tests in the contrary direction ($clade_{x\ background}$ vs $clade_y$) were significantly more similar than expected by chance in six cases (see Table 1).

Niche overlap among clades in their native and invasive range

Overall, the environmental niches in native and invasive ranges were most similar for the Eastern France Clade ($D = 0.52$, Table 2). Both niches were centered at the intersection of both axes, but the native niche was more influenced by the variable 'aridity' (Fig. 1C). Niches of the Southern Alps Clade were slightly less similar ($D = 0.4$). The potential distribution of the native Southern Alps Clade covered a large geographic range, which included all invasive occurrences (Fig. 1C). The relatively variable contribution of the SDM indicated an influence of nearly all variables, but slightly less contribution of 'annual PET' and 'mean temperature of the warmest quarter'. In contrast, the niches between native and invasive ranges of the Venetian Clade ($D = 0.27$) exhibited limited niche overlap. This clade shifted in its invasive climate characteristics along axis 1 and 2 (Fig. 1D), indicating that 'precipitation of the warmest quarter' and 'minimum temperature of the coldest month' were the underlying gradients in niche differentiation. Results of the niche similarity test based on native records compared to the invasive background of this clade revealed that *D*-values were significantly more similar than expected by chance (Table 2). Overall, the total overlap between native and invasive

occurrences of all clades was higher (mean D = 0.4) than total overlap between all native clade combinations (mean D = 0.24).

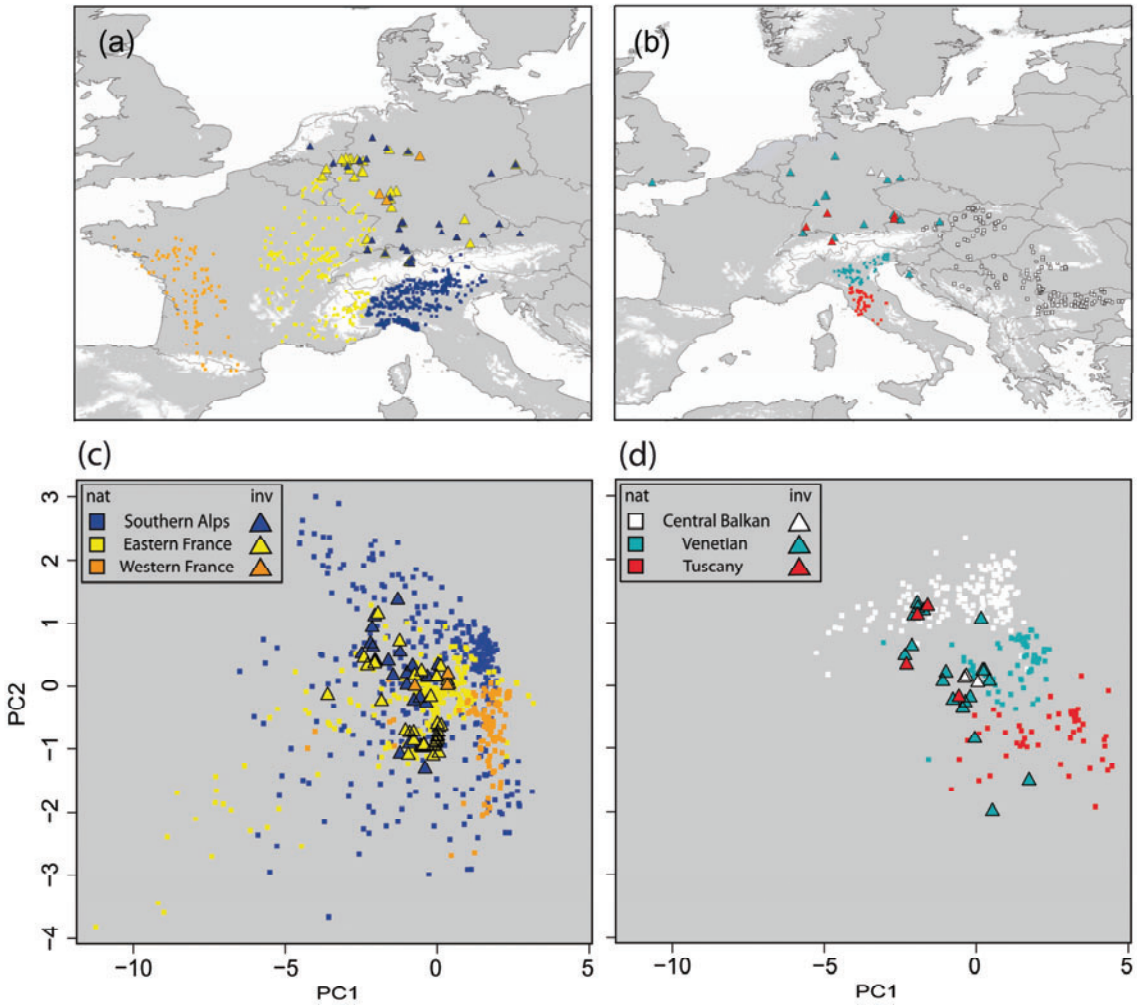

Figure 1: **(A)** Distribution of the Western France, Eastern France and Southern Alps Clades of *Podarcis muralis* in the native (= nat; rectangles) and introduced (= inv; triangles) ranges in Europe. Constraints of a clade's native range were defined by genetically analyzed records (see text). Orange symbols represent native and introduced populations of the Western France Clade (nat = 107, inv = 3), yellow symbols of the Eastern France Clade (266, 33) and blue symbols of the Southern Alps Clade (402, 32). **(B)** Distribution of the Venetian (light blue symbols, 82, 21), Tuscany (red symbols, 55, 5) and Central Balkan Clade (white symbols, 149, 3) in their native and introduced ranges in Europe. **(C)** Principal component analysis (PCA) based on six environmental characteristics at native and invasive occurrences of the clades presented in 1A (same colors). **(D)** PCA of the clades presented in 1B (same colors). The first two PCs explain ca. 81 % of the variance (PC1 = 63.58 %, PC2 = 18.27 %). The correlation circle, eigenvalues and eigenvectors are provided in Appendix S6.

Table 1: Total overlap and overlap of single niche dimensions between native clades of *Podarcis muralis*. Schoener's *D* was used as the niche overlap index. *D*-values range from 0 (no overlap) to 1 (identical species distribution models). The significance of the results is expressed by symbols.Multiple significance levels indicate niche identity tests as well as niche similarity tests in both directions. Note that niche similarity tests compare actually measured niche overlaps with null distributions based on randomizations of background data within the range of one species (i.e. clade herein). Therefore, these tests are by definition directional. Niche identity tests use a randomization between actual occurrence records and are therefore not directional.

	D total overlap	*D* aridity	*D* annual pet	*D* bio6	*D* bio10	*D* bio11	*D* bio18
Cbalk $_{vs}$ Salps	0.36$^{*,ns,\mathbf{X}}$	0.50^{*,ns,ns}	0.82$^{*,\mathbf{X},\mathbf{X}}$	0.58$^{*,\mathbf{X},\mathbf{X}}$	0.82$^{*,\mathbf{X},ns}$	0.58$^{*,\mathbf{X},\mathbf{X}}$	0.85^{*,ns,ns}
Cbalk $_{vs}$ Tusc	0.08$^{*,\mathbf{X},\mathbf{X}}$	0.79^{*,ns,ns}	0.80$^{*,ns,\mathbf{X}}$	0.10$^{*,\mathbf{X},\mathbf{X}}$	0.74$^{*,\mathbf{X},ns}$	0.24$^{*,\mathbf{X},\mathbf{X}}$	0.34^{*,ns,ns}
Cbalk $_{vs}$ Ven	0.19^{*,ns,ns}	0.65^{*,ns,ns}	0.65^{*,ns,x}	0.20^{*,ns,ns}	0.41^{*,ns,ns}	0.23$^{*,ns,\mathbf{X}}$	0.90$^{ns,ns,\mathbf{X}}$
Cbalk $_{vs}$ Wfra	0.10^{*,ns,ns}	0.59^{*,ns,ns}	0.94$^{ns,\mathbf{X},\mathbf{X}}$	0.15$^{*,ns,\mathbf{X}}$	0.57^{*,x,x}	0.16$^{*,ns,\mathbf{X}}$	0.71^{*,ns,ns}
Cbalk $_{vs}$ Efra	0.34$^{*,ns,\mathbf{X}}$	0.64^{*,ns,ns}	0.70^{*,ns,ns}	0.51$^{*,ns,\mathbf{X}}$	0.73$^{*,ns,\mathbf{X}}$	0.55$^{*,x,\mathbf{X}}$	0.86^{ns,x,ns}
Salps $_{vs}$ Tusc	0.25$^{*,ns,\mathbf{X}}$	0.64^{*,ns,ns}	0.81$^{*,\mathbf{X},\mathbf{X}}$	0.42$^{*,\mathbf{X},\mathbf{X}}$	0.82$^{ns,\mathbf{X},\mathbf{X}}$	0.56$^{*,\mathbf{X},\mathbf{X}}$	0.37^{*,ns,ns}
Salps $_{vs}$ Ven	0.33^{*,ns,ns}	0.79^{*,ns,ns}	0.53^{*,ns,x}	0.55$^{*,ns,\mathbf{X}}$	0.51^{*,ns,ns}	0.58$^{*,ns,\mathbf{X}}$	0.89$^{ns,\mathbf{X},ns}$
Salps $_{vs}$ Wfra	0.20$^{*,ns,\mathbf{X}}$	0.78$^{*,ns,\mathbf{X}}$	0.80$^{*,ns,\mathbf{X}}$	0.37$^{*,ns,\mathbf{X}}$	0.51$^{*,ns,\mathbf{X}}$	0.34$^{*,ns,\mathbf{X}}$	0.67^{*,ns,ns}
Salps $_{vs}$ Efra	0.52^{*,ns,ns}	0.84^{*,ns,ns}	0.78^{*,ns,ns}	0.81$^{*,ns,\mathbf{X}}$	0.66^{*,ns,ns}	0.83$^{*,ns,\mathbf{X}}$	0.83^{*,ns,ns}
Tusc $_{vs}$ Ven	0.20^{*,x,ns}	0.80^{*,ns,ns}	0.57^{*,ns,x}	0.48$^{*,ns,\mathbf{X}}$	0.66^{*,ns,x}	0.56$^{*,\mathbf{X},\mathbf{X}}$	0.39^{*,ns,ns}
Tusc $_{vs}$ Wfra	0.28^{*,ns,ns}	0.74^{*,ns,ns}	0.80^{*,ns,ns}	0.76^{*,ns,ns}	0.46$^{*,x,\mathbf{x}}$	0.52^{*,ns,x}	0.53^{*,ns,ns}
Tusc $_{vs}$ Efra	0.21$^{*,ns,\mathbf{X}}$	0.79$^{*,ns,\mathbf{X}}$	0.68$^{*,ns,\mathbf{X}}$	0.33$^{*,ns,\mathbf{X}}$	0.50$^{*,ns,\mathbf{X}}$	0.45$^{*,ns,\mathbf{X}}$	0.28^{*,ns,ns}
Ven $_{vs}$ Wfra	0.08^{*,ns,ns}	0.84^{ns,ns,ns}	0.64^{*,ns,ns}	0.41^{*,ns,ns}	0.16^{*,x,ns}	0.35^{*,ns,ns}	0.74^{*,ns,ns}
Ven $_{vs}$ Efra	0.24^{*,ns,ns}	0.87$^{ns,ns,\mathbf{X}}$	0.37^{*,ns,ns}	0.65^{ns,ns,ns}	0.21^{*,ns,ns}	0.56^{*,ns,ns}	0.81^{*,ns,ns}
Wfra $_{vs}$ Efra	0.26^{*,ns,ns}	0.78^{*,ns,ns}	0.69^{*,ns,ns}	0.27^{*,ns,ns}	0.63$^{*,\mathbf{X},x}$	0.26^{*,ns,ns}	0.58^{*,ns,ns}

Abbreviations: Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; Cbalk, Central Balkan; Tusc, Tuscany; Wfra,Western France; bio6, minimum temperature of the coldest month, bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter. ns, not significant; *$P < 0.05$; X = above the confidence interval (significantly more often detected than expected by chance); x = below confidence interval (significantly less often detected than expected by chance).

Comparisons of single variables among native clades

For single variables among native clades, *D* values ranged from 0.10-0.94 (Table 1). Native clades were separated mainly by temperature gradients (e.g. minimum temperature of the coldest month and mean temperature of the coldest quarter), but less so by precipitation gradients. Thus, the highest niche overlap ($D \geq 0.70$) was detected in 'aridity' (average $D = 0.74$) and 'annual PET' (average $D = 0.71$). The lowest overlap ($D \leq 0.50$) was detected in the 'minimum temperature of the coldest month' (average $D = 0.44$) and 'mean temperature of the coldest quarter' (average $D = 0.45$). The values of other variables were intermediate (Table 1). The results of an identity test among native clades revealed that most climatic conditions were significantly different. Only few clade combinations revealed similar *D*-values (e.g. in Table 1: Ven vs Wfra or Ven vs Efra for variable 'aridity').

The results of niche similarity tests based on native records compared to native background between clades showed different values for the variable 'mean temperature of the coldest quarter' followed by 'mean temperature of the warmest quarter' and 'annual PET'. Niche similarity tests revealed that the Southern Alps Clade occurred at localities with higher values of the variables

'minimum temperature of the coldest month' and 'mean temperature of the coldest quarter' (Appendix S4).

Table 2: Total overlap and overlap of single niche dimensions between native (= nat) and invasive (= inv) occurrences of clades.

	D total overlap	*D* aridity	*D* annual PET	*D* bio6	*D* bio10	*D* bio11	*D* bio18
Salps $_{nat}$ vs $_{inv}$	0.40^{*,ns,ns}	0.8^{*,ns,ns}	0.65^{*,ns,ns}	0.79^{*,ns,X}	0.55^{*,ns,ns}	0.57^{*,ns,X}	0.71^{*,x,x}
Efra $_{nat}$ vs $_{inv}$	0.52^{*,ns,ns}	0.84^{*,ns,x}	0.76^{*,ns,ns}	0.76^{ns,X,x}	0.87^{ns,X,ns}	0.74^{ns,X,ns}	0.86^{*,ns,ns}
Ven $_{nat}$ vs $_{inv}$	0.27^{*,X,ns}	0.83^{*,ns,ns}	0.40^{*,X,ns}	0.50^{*,ns,ns}	0.30^{*,X,ns}	0.47^{*,ns,ns}	0.76^{*,ns,ns}

Abbreviations: Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; bio6, minimum temperature of the coldest month; bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter. ns, not significant, $*P < 0.05$; X = above the confidence interval (significantly more often detected than expected by chance); x = below confidence interval (significantly less often detected than expected by chance).

Comparisons of single variable among clades in their native and invasive ranges

Between native and invasive clades, *D*-values ranged from 0.30 to 0.87 (see Table 2). The highest niche overlap ($D \geq 0.80$) was detected in 'aridity' (average $D = 0.82$) and 'precipitation of the warmest quarter' (average $D = 0.78$). Highly different realized niches within native and invasive ranges of clades were detected in the 'mean temperature of the warmest quarter' (average $D = 0.57$) and 'mean temperature of the coldest quarter' (average $D = 0.59$). Results of the identity tests based on native records compared to invasive records of the Southern Alps, Eastern France and Venetian Clades revealed that climatic conditions were significantly different. Only for the Eastern France Clade *D*-values of three variables 'minimum temperature of the coldest month', 'mean temperature of the warmest quarter' and 'mean temperature of the coldest quarter' were similar between native and invasive records (Table 2).

Results of the niche similarity tests based on conditions at the native records compared to the invasive background demonstrated that the Southern Alps Clade was not found at sites with low precipitation. In contrast to this, the clade was significantly less often detected in habitats with high precipitation in its native range (Table 2 and Appendix S4). The Eastern France Clade selected higher minimum temperatures of the coldest month, higher mean temperature of the warmest quarter and higher mean temperature of the coldest quarter within its invasive range than expected by chance. In its invasive range the Venetian Clade selected habitats with higher annual PET values and higher mean temperatures of the warmest quarter than expected by chance (Table 2 and Appendix S4).

Instead of computing niche comparisons between native and invasive ranges for the Tuscany, Western France and Central Balkan Clade, we visualized them using box plots, due to restricted availability of occurrence data (Appendix S4). Most strikingly, the realized native and invasive niches of the Tuscany Clades mainly differed in temperature variables, whereas native and invasive niches of the Central Balkan Clade were rather similar in temperature regime.

Potential distribution and invasion potential of different wall lizard lineages

The AUC values for the SDMs ranged from 0.958-0.990, indicating in all cases 'excellent' model performance according to the classification system of Swets (1988) (see Table 3). Overall, the potential distributions showed a strong clade-level variation. The SDM developed with native records belonging to the Eastern France Clade performed best in describing the invasive range of its analogous clade. Its potential distribution is comparatively large, ranging from the Iberian Cordillera Cantabria, the Pyrenees, central and eastern France northward up to Lower Saxony, Germany (Appendix S3). The potential geographic range includes various invasive populations in Belgium, the Netherlands and western Germany (i.e. in North Rhine Westphalia). The 'minimum temperature of the coldest month' had the highest gain for this clade, followed by 'mean temperature of the coldest quarter' (Table 3). Highly suitable areas for the Southern Alps Clade are restricted to southern Switzerland, northern Italy and eastern central Italy as well as parts of Slovenia, Croatia and adjacent Albania. Nevertheless the SDM for this clade predicted numerous invasive populations in southern Germany, Liechtenstein and Austria (Appendix S3). The most important variables for the distribution of this clade were 'mean temperature of the warmest quarter' and 'aridity'. The Central Balkan Clade has a broad potential distribution, covering large parts of the Balkans and Eastern Europe, from Bulgaria to the Czech Republic. Parts of eastern Germany were also classified as suitable and are inhabited by three invasive populations of this clade. Its geographic range model was mainly determined by 'annual PET' and 'precipitation of the warmest quarter' (Table 3).

Table 3: Importance of different variables in species distribution models (SDMs) per clade (Appendix S3) and in SDMs based on pooled data for all six clades (Fig. 2a) tested using a jackknife approach, i.e. in MAXENT SDMs each predictor was sequentially omitted or, in a second approach, used as single variable and corresponding area under the receiver operating characteristic curve (AUC) values were assessed.

variables / clades	lineages com-bined	AUC without variable	AUC with only variable	Efra	AUC without variable	AUC with only variable	Salp	AUC without variable	AUC with only variable	Ven	AUC without variable	AUC with only variable	Tusc	AUC without variable	AUC with only variable	Wfra	AUC without variable	AUC with only variable	Cbalk	AUC without variable	AUC with only variable
annual aridity	15.7	0.899	0.657	15.6	0.952	0.729	33.9	0.967	0.742	4.7	0.987	0.787	5.5	0.972	0.639	1	0.974	0.761	9	0.949	0.786
annual PET	19.6	0.902	0.769	14.5	0.951	0.801	1.9	0.97	0.786	10.3	0.988	0.931	1.3	0.974	0.782	14.4	0.961	0.825	35.5	0.948	0.831
bio 6	9.6	0.903	0.73	30.1	0.956	0.845	10.7	0.972	0.779	3	0.989	0.915	47	0.96	0.856	31.4	0.97	0.898	20.5	0.955	0.837
bio 10	12.7	0.894	0.690	10.2	0.956	0.749	37.7	0.956	0.783	38.3	0.982	0.921	18	0.96	0.822	7.5	0.958	0.85	4.3	0.951	0.732
bio11	16.3	0.901	0.744	16.2	0.956	0.834	4.2	0.971	0.784	21.7	0.989	0.927	1.3	0.966	0.842	25.7	0.97	0.92	9.5	0.954	0.841
bio 18	26.1	0.893	0.74	13.4	0.951	0.729	11.6	0.969	0.776	22	0.99	0.835	26.9	0.96	0.905	20	0.97	0.832	21.2	0.95	0.795
AUC values	0.917			0.971			0.981			0.991			0.980			0.978			0.971		

The two most important variables in each case are highlighted in grey. Abbreviations: PET, potential evapotranspiration; Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; Cbalk, Central Balkan; Tusc, Tuscany; Wfra, Western France; bio6, minimum temperature of the coldest month; bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter.

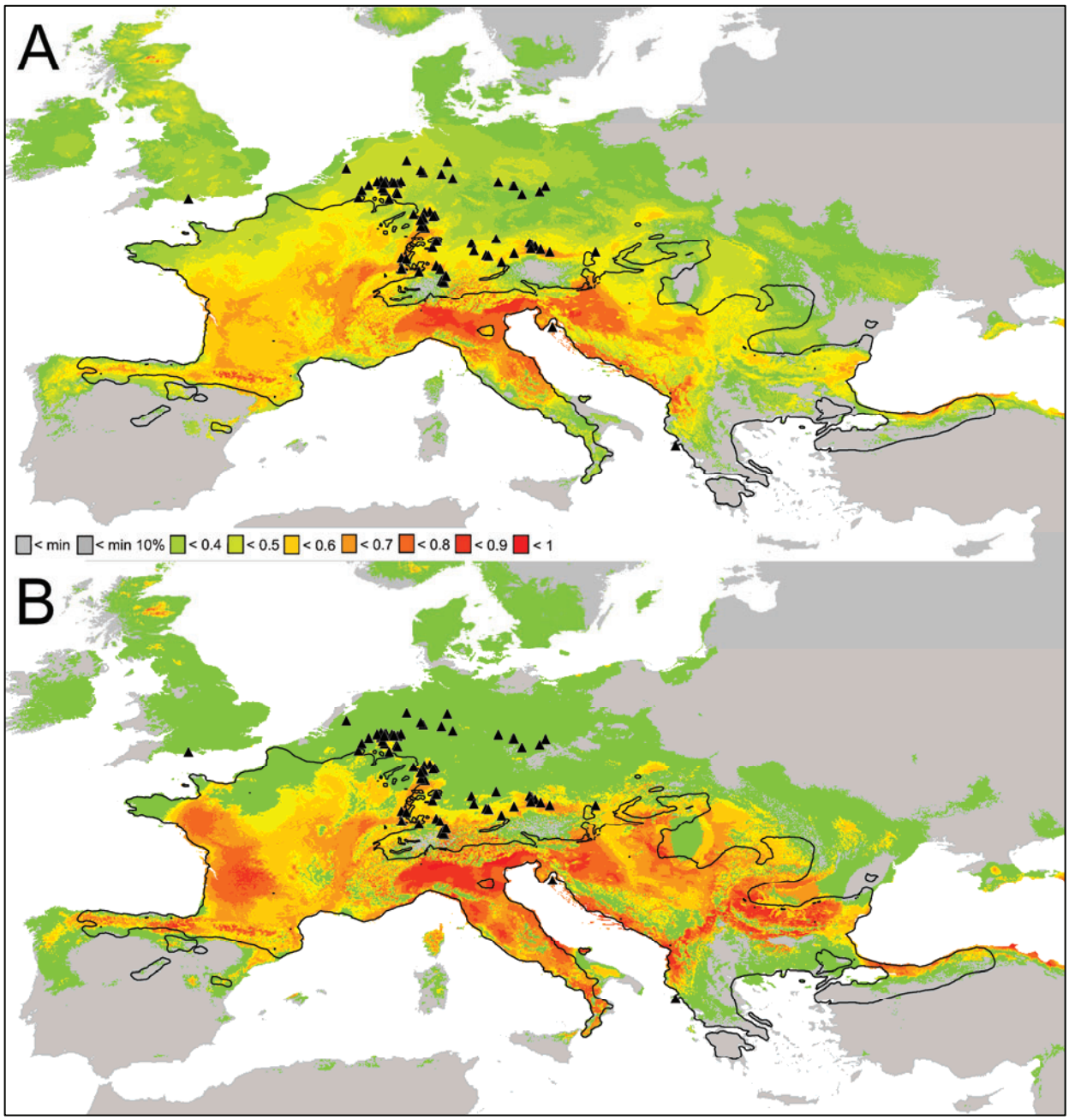

Figure 2: Potential distribution of *Podarcis muralis* predicted by climatic conditions of native occurrences of (a) of all six clades pooled and (b) as a combination of the potential distributions of each lineage by computing the maximum prediction per grid cell. For native records of the six clades see Figure 1 (a, b). Invasive populations are indicated as black triangles. Warmer colors correspond to higher occurrence probabilities. The whole distribution range is framed by a solid black line.

In contrast to these well matching SDMs, the models failed to predict the current invaded distribution for the Venetian, Tuscany and Western France Clade (Appendix S3). Climatically suitable areas for the Venetian Clade were restricted to northern Italy, the Eastern Po valley up to the border of Slovenia. The most important variables describing the distribution of this clade were 'mean temperature of the warmest quarter' and 'precipitation of the warmest quarter'. Areas with the highest climatic suitability for the Tuscany Clade encompass Italy, beside the Abruzzi and large parts of the Mediterranean and Black Sea coasts. Climatically suitable areas for the Western France Clade are restricted to the Basque Country,

western Pyrenees and western France up to the Massif Central (Appendix S3). Important variables explaining the distribution of these clades are given in Table 3.

The sum of single SDMs for all six clades (Fig. 2B) compared to the SDM for the species using all records pooled (Fig. 2A) revealed largely overlapping potential distributions (D = 0.83; simple linear regression R^2 = 0.760, P < 0.0001), wherein the model built by pooling data from all lineages performed better than the one combining the models from each lineage. Both models mainly predicted the invasive populations in western and southern parts of Central Europe, whereas they failed to predict those populations in the northern and north-eastern parts (Fig. 2A/B).

Discussion

Origin of invasive wall lizard populations

We assigned 77 % of all currently known invasive wall lizard populations in Central Europe apart from the UK to eight source lineages based upon their mitochondrial haplotypes and an extensive phylogeography covering the entire range of the species (Giovannotti *et al*. 2010; S. S. *et al*., unpublished data). Introduced populations of the same lineage sometimes occurred in close proximity, indicating human-facilitated jump dispersal. On the other hand, we also found 19 introduced populations with haplotypes belonging to different lineages, indicating multiple introductions of wall lizards from different source populations (Appendix S7). In such mixed populations hybridization may promote the invasion success due to heterosis (Kolbe *et al*. 2004). Interestingly, we even discovered the haplotype of the alien *Podarcis liolepis* at one location in southern Lower Saxony (Appendix S7) together with haplotypes of the Western France *P. muralis* Clade. Both species naturally co-occur across parts of the Eastern Pyreneans. It is, therefore, likely that haplotypes of both species have been translocated from this region simultaneously.

Niche differentiation among native clades

We found strong intra-specific variation in the realized niches among native clades, mainly based on temperature gradients. Realized niche differentiation was associated with geographic distance among clades. The two most similar clades (Eastern France and Southern Alps) occur in adjacent regions and together form the species' northern range border in western Central Europe. Within its native range, the Southern Alps Clade occurs at sites with higher minimum temperatures of the coldest month and higher mean temperatures of the coldest quarter compared to native background. This may be due to the strong altitudinal gradient within its native range and its need for successful hibernation and partial winter activity (Schulte 2008). In contrast, the geographically widely separated Central Balkan and Tuscany Clades differed strongly in their realized climatic niches. Niche overlap and background tests of single variables indicated that both clades occur in areas that clearly differ in their minimum temperature of the

coldest month and the mean temperature of the coldest quarter. The range of the Central Balkan Clade is also largely influenced by the annual PET. It is known that this lineage occurs in wetlands and humid oak forests of the Bulgarian Dobruja and avoids xeric habitats (Schulte 2008). The distribution of the Tuscany Clade is mainly influenced by lower mean temperatures of the warmest quarter. This may be explained by the Mediterranean climate, where the lizards need to sustain hot and dry periods in the summer by inhabiting shady and humid habitats with dense vegetation (Capula *et al*. 1993).

Niche overlap between native and invasive populations

Differentiation in realized niches between native and invasive populations within clades was on average lower than among native populations of different clades. In particular, the realized climatic niches of the native and invasive ranges of each the Southern Alps and the Eastern France Clade were rather similar. Nevertheless, niche similarity tests based on single variables also revealed some differences. For example, records of the Southern Alps Clade were not related to high precipitation in the native range but in the invasive range. This may reflect a shift in habitat affiliation rather than differences in the availability of habitats in the novel range. Niche similarity tests for the Eastern France Clade within its invasive range revealed that minimum temperature of the coldest month, mean temperature of the warmest quarter and mean temperature of the coldest quarter were explaining most of the variability. This corresponds to both the need of high temperatures during early summer for reproduction and the need for successful hibernation and partial winter activity (Barbault and Mou 1988). Similarly, invasive populations of the Venetian Clade were mainly recorded from sites with higher mean temperatures of the warmest quarter than expected by chance. Mean temperatures of the early summer are of major importance for the reproductive success of this oviparous lizard at its northern range border as they strongly affect incubation time (in the wild: 6-11 weeks) and hatchling phenotype (Braña and Ji 2000). In the northernmost native population of this clade (Maastricht), cold and rainy summers can cause almost complete hatching-breakdowns (Stumpel 2004). The Venetian Clade had the lowest niche overlap between its native and invasive range. In its invasive range, this clade occurs in areas with higher annual PET and higher mean temperatures of the warmest quarter. High values of both variables are typically found within its native range and are known to contribute to reproductive success and microhabitat selection (Mazzotti 1999). Overall, the invasive distribution of the Venetian Clade and the low niche overlap between native and invasive ranges suggest that the fundamental niche of this clade might be larger than the niche realized in its actual native range.

Furthermore, it has to be considered that systematic human-mediated introductions of lizards into highly suitable habitats took place. Hence, the lizards were brought into areas that represent local extremes within the regional climate (e.g. water-filled quarries). Moreover, the introduction of lizards is influenced by the usual human travel routes. It is apparent that the Central Balkan clade was only found in eastern Germany. Citizens of the former German Democratic Republic were not able to travel abroad, except for some other countries of the Eastern Bloc. Hungary was one of the most popular travel

destinations and, indeed, the haplotypes found in invasive populations of the Central Balkan clade were very similar to those found in Hungarian native populations. On the other hand, it is striking that clades from the southernmost part of the range of *P. muralis* were not recorded in Central Europe, although at least Greece is a popular travel destination.

The cryptic niche conservatism hypothesis

The SDMs revealed clear inter-clade differences in the realized niches, but for some evolutionary lineages the models failed to predict the invasive range. The best predictive power was found for those clades that most frequently colonized Central Europe (Eastern France and Southern Alps Clades). However, the native ranges of these two clades are also spatially closest to Central Europe, which might increase the climatic overlap with the invasive range. Hence, it is likely that these clades might have been pre-adapted to the environmental conditions in Central Europe. Both clades possess a broad thermal tolerance (Appendix S4), leading to a large potential invasive distribution (Appendix S3). Although the Southern Alps Clade is naturally restricted to a rather small native range mainly south of the Alps, it occurs in a complex climate due to the great altitudinal gradient in this area. Populations of this clade have been reported up to 1,770 meters above sea level (Hofer *et al*. 2001) and experiments in cooling chambers demonstrated a moderate freeze tolerance (Claussen *et al*. 1990).

SDMs for the Venetian, Tuscany and Western France Clades failed to predict the invasive ranges. Despite a narrow realized niche of its native range, the Venetian Clade colonized areas in Central Europe (Appendix S3). Two hypotheses may explain this phenomenon: (1) a shift in the fundamental niche during the invasion process (niche shift hypothesis) or (2) the available climate space within its native range does only reflect a part of the fundamental niche (cryptic niche conservatism hypothesis). The fact that the distribution of the Venetian Clade is strongly restricted by neighboring conspecific clades and other *Podarcis* species supports the second hypothesis. The same is true for the Western France Clade and for the Tuscany Clade.

Our results suggest that climate adaptations of the studied lineages are not strong enough to prevent them from becoming invasive, even if this would not be expected based upon their realized niche. However, the invaded areas were covered in SDMs for other lineages and for the complete data set. This suggests that modelling only one lineage might lead to wrong conclusions. It might well be true that reported niche shifts during species' invasions (Broenniman *et al*. 2007, Treier *et al*. 2009) simply reflect cryptic such niche conservatism on a higher systematic level (i.e. genus level).

Conclusions

Niche conservatism has been reported in many species and even genera (Peterson *et al*. 1999, Peterson & Holt 2003, Pearman *et al*. 2008). Our models revealed a strong niche differentiation among clades and mismatches between the realized niches in the native and invasive ranges, as recently reported also for

other invasive species (Broenniman *et al*. 2007, Rödder & Lötters 2009, Treier *et al*. 2009). Based upon SDMs it is impossible to disentangle whether such patterns represent shifts in the realized niche only or in both the realized and the fundamental niche (Broenniman *et al*. 2007, Rödder *et al*. 2010). SDMs simply match species distributions with climate variables and do not integrate scenopoetic or bionomic variables (e.g. competition, predation, dispersal; variables of the Eltonian niche; Soberón 2007). Such models might thus fail to predict the invasive range, particularly, if the native range size is rather small and a great part of the fundamental niche is hidden. This means that a small (realized) niche may hide a broad (fundamental) niche (cryptic niche conservatism).

Our results have important implications for the interpretation of geographic predictions for invasive species based upon SDMs. Although evolutionary lineages within a species may have distinct realized niches, these do not necessarily imply a niche differentiation. They might thus become invasive outside their native realized niches. On the other hand, using the pooled records of invasive clades performs much better in predicting the invasion risk (Fig. 2A). Hence, building models for evolutionary lineages will not necessarily improve SDM predictions. Further studies should address the general validity of these patterns on different evolutionary time scales (divergence times) and distribution patterns of species (Peterson and Holt 2003). Understanding intraspecific niche evolution might be crucial for a more reliable risk assessment of invasive species as well as climate change impacts on taxa.

Acknowledgements

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Supporting Information

Appendix S1. Additional references from which species records were obtained.

Appendix S2. References from which invasive records were obtained.

Appendix S3. Potential distribution of clades predicted by climatic conditions within their native range and predicted by climatic conditions within their invasive range.

Appendix S4. Comparison of bioclim variable scores at native and invasive occurrences and within native and invasive background of clades.

Appendix S5. Comparison of bioclim variable scores at native and invasive occurrences of the Tuscany, Western France and Central Balkan Clade.

Appendix S6. Correlation circle, eigenvalues and eigenvectors of the Principal Components Analysis (PCA).

Appendix S7. Invasive populations sampled with information on locality, coordinates, sample size, clade affiliation and references.

Appendix S8. Phylogenetic tree for the assignment of invasive haplotypes to intraspecific evolutionary *P. muralis* lineages.

BIOSKETCHES

This study is part of the PhD thesis of **Ulrich Schulte**, who is interested in biological invasions and conservation biology. He combines molecular genetic techniques with niche modelling to develop a differentiated risk assessment for invasive species.

Appendix S1: Species records were obtained from the following references and from personal communication with Franzen 2007, Tudor and Cogălniceanu 2007, and Verneck 2007:

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Appendix S2: Invasive records were obtained from the following references:

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Appendix S3

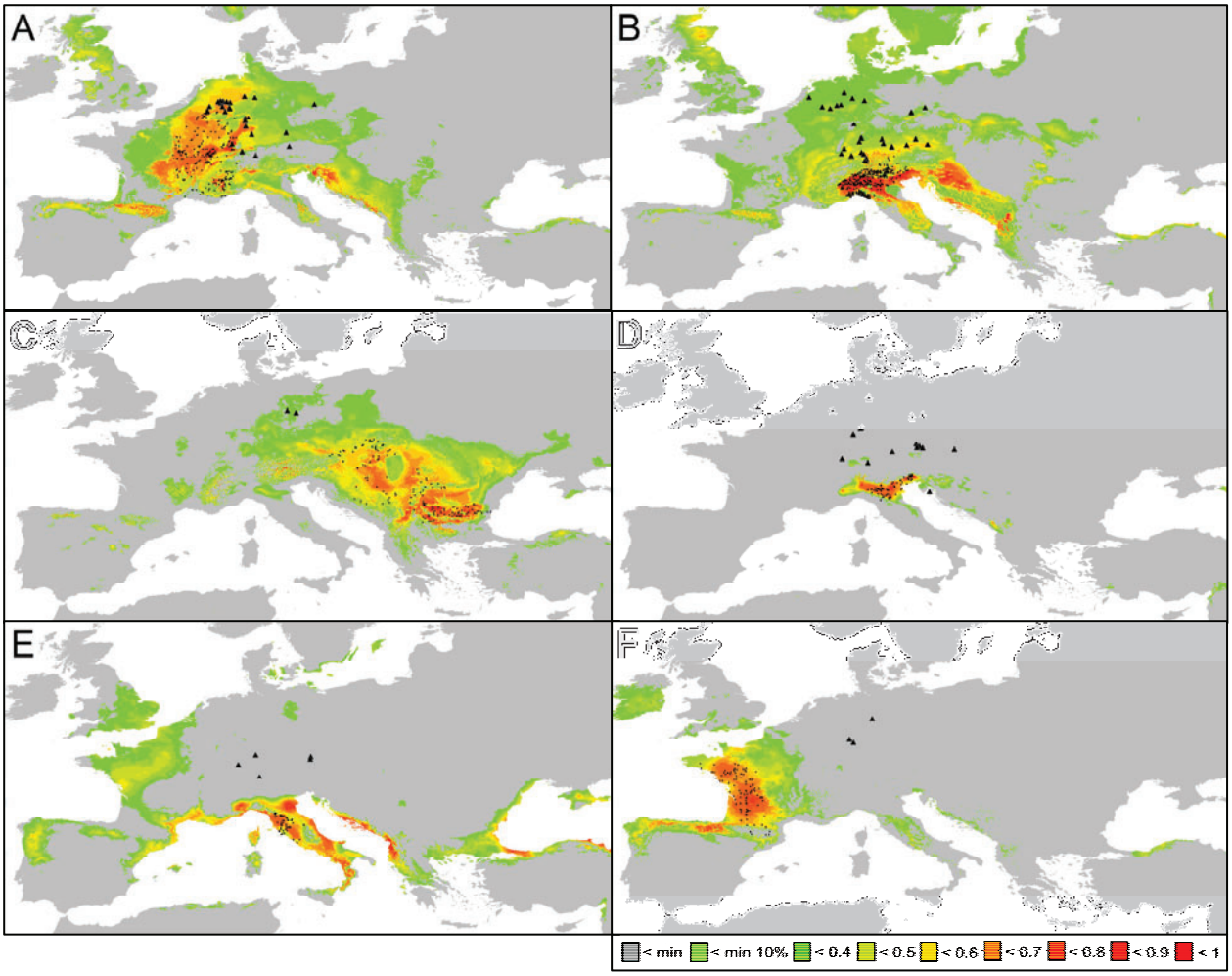


Fig. 3: Potential distribution of clades predicted by climatic conditions within their native range. Native records are indicated as black dots, invasive populations as black triangles (A: Eastern France Clade, B: Southern Alps Clade, C: Central Balkan Clade, D: Venetian Clade, E: Tuscany Clade, F: Western France Clade). Warmer colors correspond to higher occurrence probabilities.

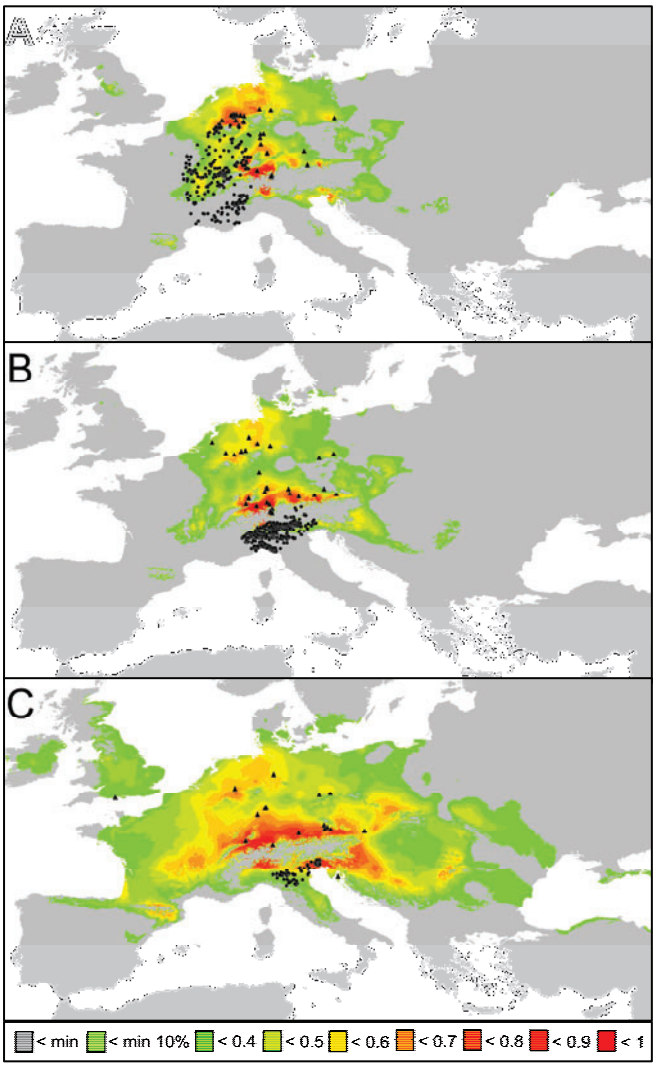


Fig. 4: Potential distribution of three clades with strong invasive occurrence predicted by climatic conditions within their invasive range. Native records are indicated as black dots, invasive populations as black triangles (A: Eastern France Clade, B: Southern Alps Clade, C: Venetian Clade). Warmer colors correspond to higher occurrence probabilities.

Appendix S4

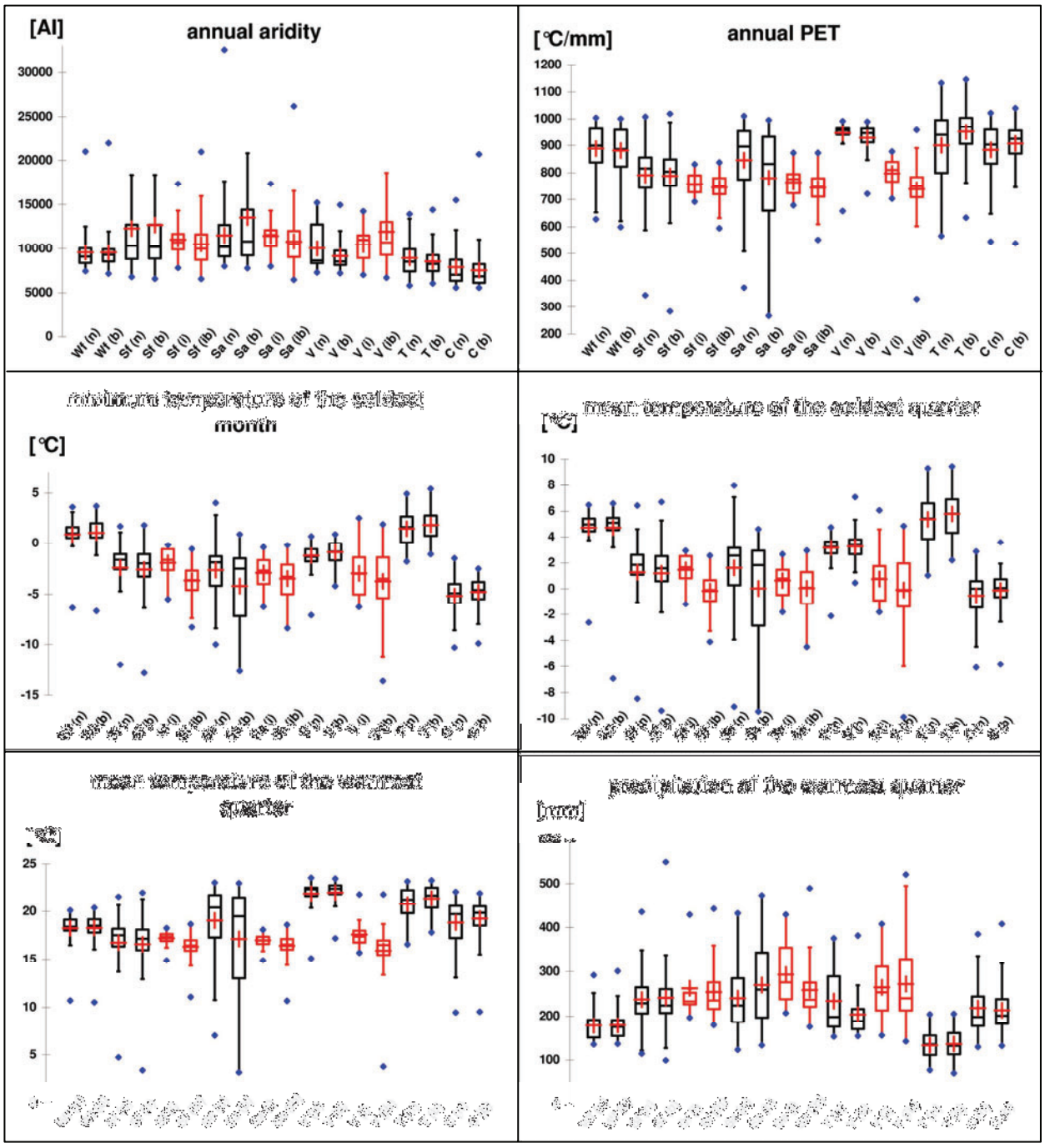


Fig. 5: Comparison of six bioclimate variable scores at native (n) and invasive (i) occurrences and within native (b) and invasive (ib) background. Background points used were randomly chosen within the native and invasive areas enclosed by a minimum convex polygon (MCP) for each clade. Conditions within the range of three clades with strong invasive occurrence are highlighted in red. Abbreviations: Sa = Southern Alps, Sf = Eastern France, V = Venetian, C = Central Balkan, T = Tuscany, Wf = Western France Clade.

Appendix S5

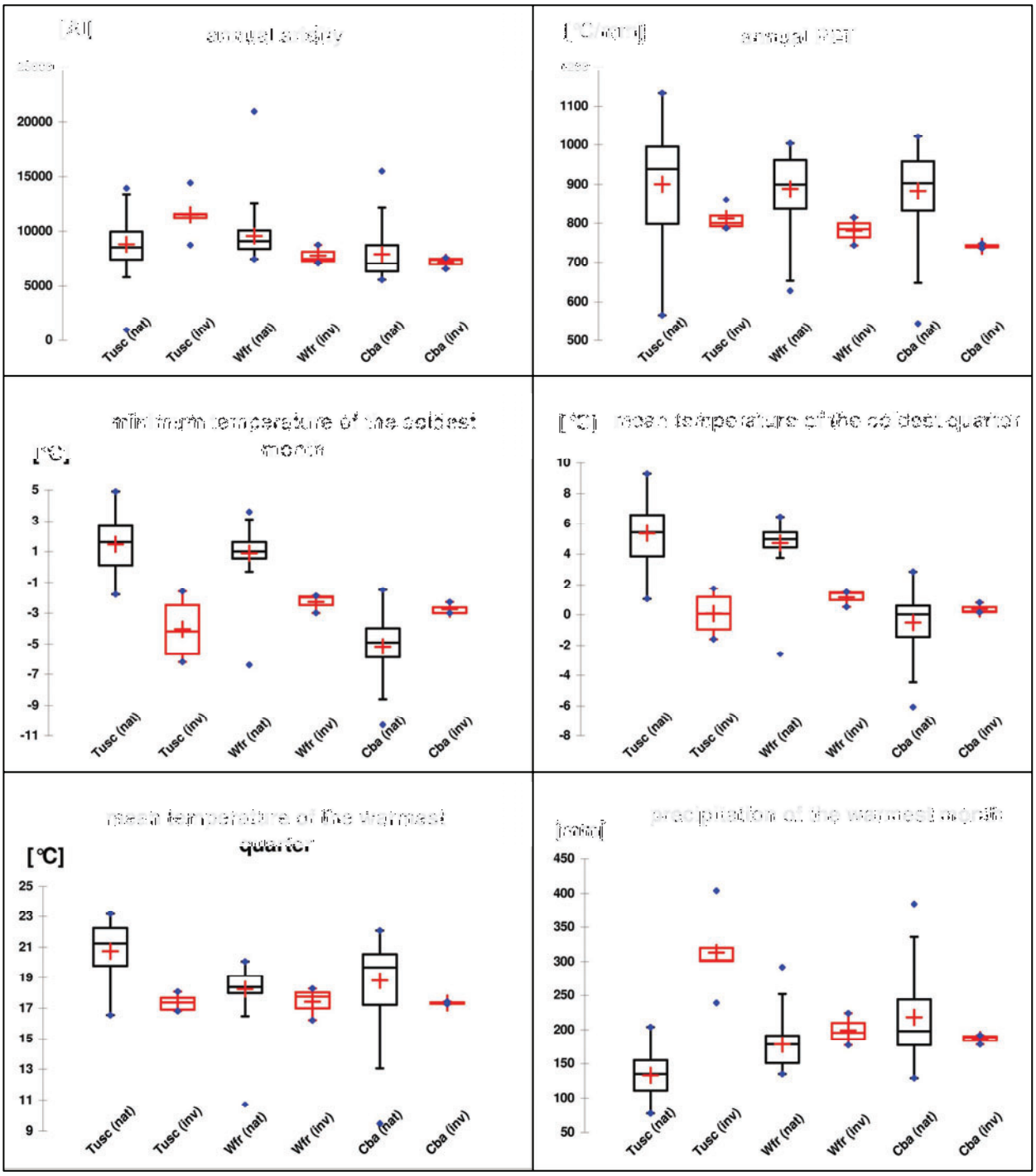


Fig. 6: Comparison of six bioclimate variable scores at native (nat) and invasive (inv) occurrences of Tuscany (Tusc), Western France (Wfr) and Central Balkan Clade (Cba).

Appendix S6. Correlation circle, eigenvalues and eigenvectors of the Principal Components Analysis (PCA).

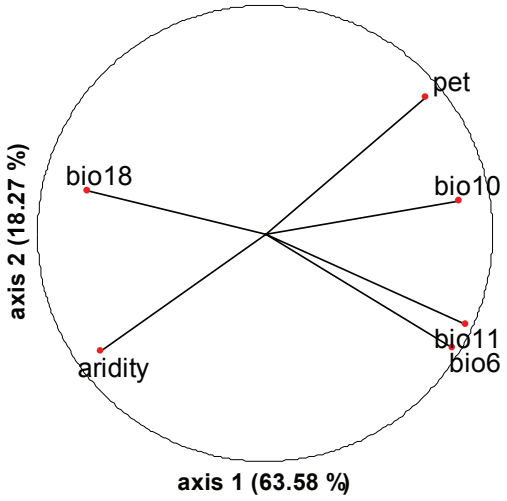


Fig. 7: Correlation circle illustrating the correlation of climatic variables with PCs (= axes).

Table 6: Eigenvalues of the Principal Components Analysis (PCA).

	F1	F2	F3	F4	F5	F6
eigenvalue	3.82	1.10	0.53	0.30	0.22	0.03
variability (%)	63.58	18.27	8.88	4.50	3.72	0.57
cumulative %	63.58	81.85	90.73	95.71	99.43	100.00

Table 7: Eigenvectors of the Principal Components Analysis (PCA).

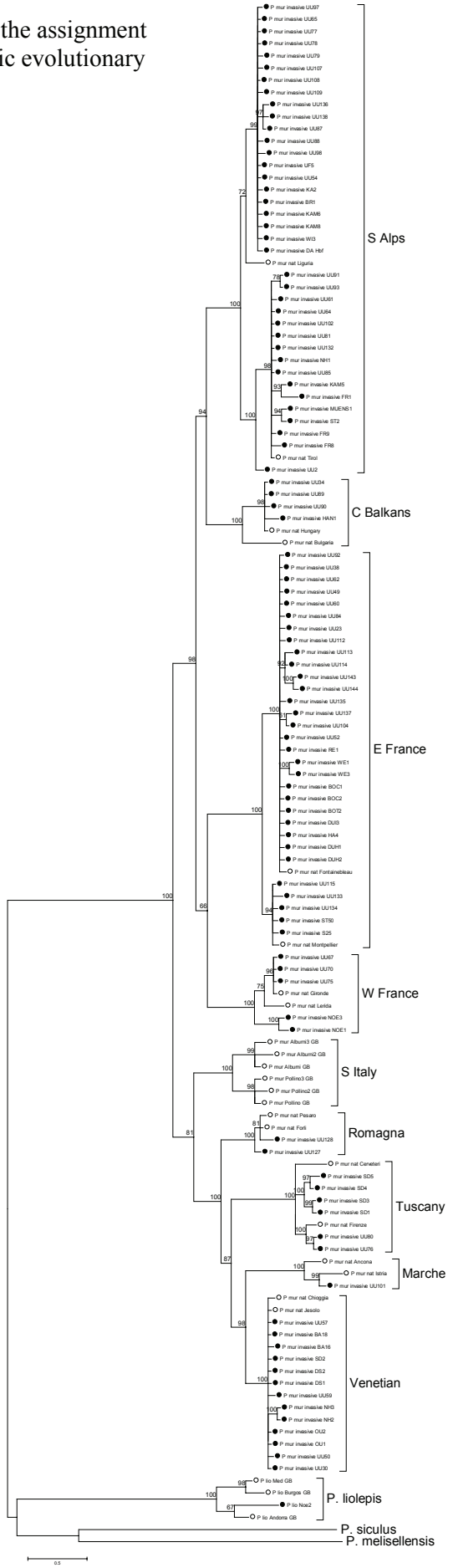
	F1	F2	F3	F4	F5	F6
aridity	-0.37	-0.49	0.40	0.53	0.42	-0.05
bio6	0.42	-0.48	0.10	-0.37	0.09	-0.66
bio10	0.44	0.13	0.45	0.52	-0.55	-0.12
bio11	0.45	-0.39	0.23	-0.22	0.09	0.74
bio18	-0.40	0.18	0.71	-0.52	-0.18	-0.02
PET	0.36	0.57	0.26	0.04	0.69	-0.07

Appendix S7: Table 8: Invasive populations sampled as well as populations for which reliable information on their origin was available with information on locality, coordinates, sample size, clade affiliation and references. Abbreviations: Salps = Southern Alps, Efra = Eastern France, Ven = Venetian, Cbalk = Central Balkan, Tusc = Tuscany, Wfra = Western France Clade.

Locality	Latitude	Longitude	Sample size	Clade	Reference
Germany					
1. NS, Bramsche	52,4424085	7,8758239	2	Salps	
2. NS, Nörten-Hardenberg	51,6303786	9,9357604	5	Wfra/*P. liolepis*	
3. NS, Hannover-Berggarten	52,3943537	9,6986961	3	Ven	
4. NRW, Bielefeld	52,0043285	8,4994697	1	Salps	
5. NRW, Schloss Holte-Stukenbrock	51,9063664	8,6101913	2	Efra	
6. NRW, Dortmund, Hengsteysee	51,4189074	7,4739646	2	Efra	
7. NRW, Kamp-Lintfort	51,4942097	6,5481948	1	Efra	
8. NRW, Duisburg Hüttenheim	51,3694227	6,7313575	1	Efra	
9. NRW, Duisburg-Ruhrort	51,4555044	6,7332458	0	Efra	pers. Comm.
10. NRW, Duisburg-Hochfeld	51,4180509	6,7533302	2	Efra	
11. NRW, Duisburg-Innenhafen	51,4428807	6,7627716	3	Efra	
12. NRW, Dinslaken	51,5527397	6,7239761	1	Efra	
13. NRW, Bonn-Poppelsdorf	50,7222208	7,0890998	0	Efra	pers. Comm.
14. NRW, Holzwickede	51,5010492	7,62331	1	Salps	
15. NRW, Witten-Bommern	51,420192	7,3380088	1	Salps	
16. NRW, Witten-Heven	51,4341062	7,3057365	3	Salps	
17. NRW, Bochum Bot. Garten	51,4819708	7,2159147	2	Efra	
18. NRW, Bottrop	51,5211343	6,9467926	3	Efra	
19. NRW, Oberhausen	51,4938891	6,8736648	1	Efra	
20. NRW, Kaldenkirchen	51,3267501	6,1804962	2	Salps	
21. NRW, Mülheim a. d. R.	51,4188538	6,8675708	2	Ven	
22. NRW, Düsseldorf Bot. Garten	51,1924697	6,7979621	1	Salps	
23. NRW, Monheim	51,0842237	6,8853378	3	Efra	
24. NRW, Remshagen	51,0216918	7,4249553	2	Efra	
25. NRW, Weiershagen	50,9652111	7,4629783	3	Efra	
26. NRW, Stahle	51,8357775	9,4290161	2	Efra/Salps	
27. SA, Halle a. d. S.	51,4768926	11,974411	2	Cbalk	
28. SN, Dresden	51,0422573	13,833847	2	Ven	
29. SN, Ammelshain	51,2981008	12,6420021	1	Cbalk	
30. SN, Altenhain	51,3013207	12,6823425	2	Cbalk	
31. SN, Kamenz	51,2760919	14,0942573	8	Salps/Efra	
32. SN, Frankenberg	50,9116924	13,033905	2	Salps/Ven	
33. HE, Frankfurt	50,1070382	8,672676	1	Efra	
34. HE, Hanau	50,1331238	8,911457	4	Efra	
35. HE, Darmstadt, Bessungen	49,8286816	8,6594581	4	Efra/Efra (Languedoc)	
36. HE, Darmstadt Hbf	49,872402	8,6304473	1	Salps	
37. HE, Gernsheim	49,7558743	8,4889984	2	Wfra	
38. RP, Mainz	50,0198179	8,1832695	3	Wfra	
39. BW, Mannheim	49,4851894	8,512001	1	Ven	
40. BW, Heidelberg	49,4170039	8,7075233	0	Efra	Baier (2008)
41. BW, Tübingen (Spitzberg)	48,5173434	9,0377998	1	Salps	
42. BW, Stuttgart Birkenkopf	48,7652981	9,1316986	3	Salps	
43. BW, Stuttgart, Kriegsberge	48,7959523	9,1756439	2	Efra	
44. BW, Stuttgart, Schiffländе	48,8031395	9,2104911	9	Tusc/SAlps	
45. BW, Stuttgart, Travertinpark	48,7994012	9,1975736	3	Efra (Languedoc), Salps	
46. BW, Stuttgart, Bad Cannstatt	48,7866364	9,2452955	7	Efra (Languedoc), Efra,	
47. BW, Freiburg	47,9909089	7,8621178	10	Salps/Tusc	
48. BW, Ihringen	48,0418528	7,6427507	0	Efra	Laufer et al. 2007
49. BW, Mainau	47,7045345	9,2003095	1	Salps	
50. BW, Inzlingen	47,587468	7,6795291	2	Ven/Salps	
51. BW, Lörrach Stetten	47,6045643	7,6518917	5	Salps/Romagna	
52. BY, Augsburg	48,3652311	10,8859491	1	Salps	

Locality	Latitude	Longitude	Sample size	Clade	Reference
53. BY, Neuötting	48,2436533	12,6821708	2	Salps	
54. BY, Obernzell	48,5568413	13,62957	2	Ven	
55. BY, Passau-Grubweg	48,5766071	13,4767913	2	Ven	
56. BY, Tittling	48,7278882	13,3808326	5	Salps/Ven	
57. BY, Hutthurm	48,671466	13,4706115	1	Tusc	
58. BY, München Aubing	48,1633374	11,4276695	1	Marche	
59. BY, München Südbahnhof	48,1217572	11,5536689	1	Salps	
60. BY, München Donnersberger Brü.	48,1430092	11,5345277	3	Salps/Ven	
61. BY, Rosenheim	47,8520467	12,11483	2	Efra	
62. BY, Kelheim	48,9140389	11,8751907	1	Efra	
63. BY, Aschaffenburg, Pompejanum	49,9778318	9,1393375	1	Ven	
64. BY, Aschaffenburg Hbf	49,9391651	9,063611	3	Ven	
65. BY, Donauwörth	48,7156574	10,7726955	1	Salps	
Austria					
66. O, Urfahr	48,3051778	14,2818832	1	Salps	
67. O, Schlögen	48,4242454	13,8728141	2	Ven	
68. O, Schärding	48,4604294	13,4316015	6	Tusc/Ven	
69. N, Klosterneuburg	48,2993755	16,3336122	2	Ven	
70. V, Feldkirch	47,2375491	9,5931673	1	Salps	
71. V, Rankweil	47,2725903	9,6377992	1	Ven	
Liechtenstein					
72. Vaduz	47,1444304	9,5084953	1	Efra	
73. Triesen	47,1113782	9,5191383	0	Salps	Kühnis 2008
Switzerland					
74. Basel-Riehen	47,5783351	7,6335883	3	Romagna	
75. Basel-Wiesenmatte	47,5866647	7,6416993	4	Ven/Romagna	
76. Basel, Bot. Garten	47,5333711	7,6145982	2	EFra/Ven	
77. Buchs	47,4544425	8,4313201	2	Salps/Efra	
78. Autal	47,5841175	7,6660215	2	Ven	
79. Trübbach	47,0657956	9,4681763	1	Efra	
80. Bad Ragatz	47,0109572	9,5039033	2	Efra/Tusc	
81. Sargans	47,0477856	9,4335651	2	Salps/Efra	
82. Romanshorn	47,5632645	9,3801784	1	Salps	
Netherlands					
83. Echt	51,0972697	5,872364	0	Efra	Jeroen van Delft
England					
84. Bournemouth	50,721297	1,8926525	0	Ven	Deichsel et al. 2007
Croatia					
85. Cres	44,9602279	14,4051146	0	Ven	Mayer, pers. comm.

Appendix S8. Phylogenetic tree for the assignment of invasive haplotypes to intraspecific evolutionary *P. muralis* lineages.



CHAPTER II

Buccal swabs as a reliable non-invasive tissue sampling method for DNA analysis in the lacertid lizard *Podarcis muralis*

Schulte, U., Gebhard, F., Heinz, L., Veith, M. & A. Hochkirch (2011): Buccal swabs as a reliable non-invasive tissue sampling method for DNA analysis in the lacertid lizard *Podarcis muralis*. – *North-Western Journal of Zoology* 7(2): 325-328.

Abstract: We tested the performance of buccal swabs for microsatellite analysis in an introduced population of the Common Wall Lizard (*P. muralis*) in Germany. The quantity and quality of the isolated DNA collected by buccal swabbing and by screwing a tail tip of the same individuals was compared. Although the DNA yield from buccal swabs was much lower than from tissue, it was sufficient for a successful amplification. We genotyped the individuals at two microsatellite loci. Buccal swabs generated genotypes just as well as tissue samples. We could not find a lower threshold of DNA quantity that increased genotyping errors. In contrast, very high DNA yields (>10 ng/ml), as found in some tissue samples, produced a higher number of unspecific peaks. These results show that buccal swabs are a simple and efficient non-invasive sampling method for DNA analysis in adult lacertid lizards. Carefully applied the technique does not harm the specimens in their locomotor performance and energy reserves. An additional advantage of buccal swabbing is the time-saving DNA extraction, since there is no need to remove scales, chop up the tissue and also not for a long digestion step.

Key words: conservation genetics, DNA extraction, genotyping, microsatellite, non-invasive sampling, *Podarcis muralis*

During recent decades, the availability and use of microsatellites as marker system for population genetic studies has strongly increased (Selkoe & Toonen, 2006). Microsatellites are particularly suitable to gain insights into fine-scale processes in conservation genetics, such as inbreeding depression, hybridization and consequences of habitat fragmentation. Tissue sampling (toes and tail tips) is often considered the most reliable technique to gain DNA-templates for genetic analyses in amphibians and reptiles. Ethic concerns about animal welfare and conservation (May 2004, Funk et al. 2005) fostered the search for alternative non-invasive methods that do not harm individuals (Pidancier et al. 2003). Buccal swabbing has recently been suggested as a routine non-invasive technique to gain DNA-templates from amphibians (Broquet et al. 2007) and reptiles (Miller 2006).

Nevertheless, genetic analyses using buccal swabs are still very scarce, particularly among lacertid lizards (Beebee 2008). This is caused by the naturally high tail autotomy rates within lizard populations that make tail tips as tissue samples ethically justifiable. However, it is has been shown that caudal autotomy reduces arboreal locomotor performance in climbing lizard species, since the tail serves as a counterbalance (Brown et al. 1995). Furthermore, the tail serves as an important lipid energy reserve for hibernation and autotomy may, therefore, be energetically costly.

We tested the performance of buccal swabs for DNA analysis in an introduced population of the Common Wall Lizard (*P. muralis*) in Germany. We compared the quantity and quality of the isolated DNA collected by buccal swabbing and by screwing a tail tip of the same individuals. We than genotyped the individuals at two randomly chosen microsatellite loci. We sampled 49 adult lizards (Snout-Vent Length ≥ 50mm) from an introduced wall lizard population in Dresden, Saxony. Lizards were captured by hand or by noosing in August 2009. No lizard displayed autotomy while catching. Sampling of buccal cells was carried out using a diagnostic fine-tip dry swab (Medical Wire & Equipment, MW-100) by comprehensively swabbing each specimen underneath its tongue and cheek for about a minute. Nearly all individuals bit voluntarily into the swabs. Samples were stored in sterile tubes at -20°C until DNA extraction. DNA was extracted using the Qiagen DNEasy blood and tissue kit following the manufacturer's protocol (adding PBS buffer). For comparison a small tail tip (5 mm length) of the same individuals was screwed until autotomy occurred. Individuals were immediately released after sampling. Tissue samples were stored in 99% ethanol p.a. at room temperature until DNA extraction. After removing scales, DNA was extracted from muscle tissue of tail tips using the Qiagen DNEasy blood and tissue kit.

Total DNA yield obtained from swabs and tissue was quantified with a Qubit® Fluorometer (Invitrogen) and compared with a paired t-test. To test the reliability of DNA templates for microsatellite genotyping, we genotyped all specimens at two loci using primers specifically developed for *Podarcis muralis* (C8f: FAM-GACAATCCAATGTACAGAGCAAG, C8r: AACACACATGCACAAACCAC; B4f: HEX-AATCTGCAATTCTGGGATGC, B4r: AGAAGCAGGGGATGCTACAG; Nembrini & Oppliger 2003). For the PCR reactions we used three different templates: i) DNA from tissue diluted 1:10

with ultrapure water, ii) undiluted DNA from swabs for the twelve samples with the lowest DNA yield and iii) swabs diluted 1:10 with ultrapure water. PCR amplification was performed in a 20 µl reaction volume containing 8 µL 5Prime HotMasterMix, 10 µl ultrapure water and 0.5 µl of the forward and reverse primers, respectively. PCR amplifications were performed in a Multigene Gradient Thermal Cycler (Labnet) using the following profile: initial denaturation of template DNA for 2 min at 94°C; 35 cycles for 30 s at 94°C, 50 s at 57°C and 45 s at 65°C; and a final extension of 3 min at 65°C. PCR products were genotyped on a MegaBACE 1000 automated sequencer (GE Healthcare). We used FragmentProfiler 1.2 (Amersham Biosciences) for scoring the data. We compared the results of allele lengths, the number of amplification failures and the occurrence of unspecific peaks between swab and tissue samples and between loci (χ^2 cross tabulation test). To test for differences in the number of unspecific peaks between loci, we used Fisher's Exact Test, as the expected value for one locus was smaller than five. Peak heights were compared among sampling techniques by calculating the mean peak height per individual and locus. We first performed an ANCOVA with the explanatory variables "locus" and "sampling method" and the covariate "DNA content". As we found a significant interaction between sampling method and DNA content, we tested for correlation between peak height and DNA content separately for both loci and sample methods using a linear regression model. A similar procedure was performed to evaluate whether the occurrence of unspecific peaks is correlated with the sampling method, locus or DNA content. Due to the binomial data format (unspecific peaks present = 1, not present = 0), we used a Generalized Linear Model with binomial error distribution. Afterwards, we simplified the model using the step function in R. All statistical analyses were performed in R 2.12.0 (R Development Core Team 2010).

The DNA yield obtained from tissue was significantly higher than from swabs of the same individuals (paired t-test, df = 48, t = 9.75, $p < 0.001$; Fig. 1). Scoring results were identical among swab and tissue samples for all individuals. Amplification failed significantly more often in locus C8 than in locus B4 (χ^2 cross tabulation test, $\chi^2 = 6.27$, df = 1, p = 0.01), but was not influenced by sampling method (B4: χ^2-test, $\chi^2 = 0.1$,, df = 1, p = 0.76; C8 = χ^2-test, $\chi^2 = 0.21$, df = 1, p = 0.65).

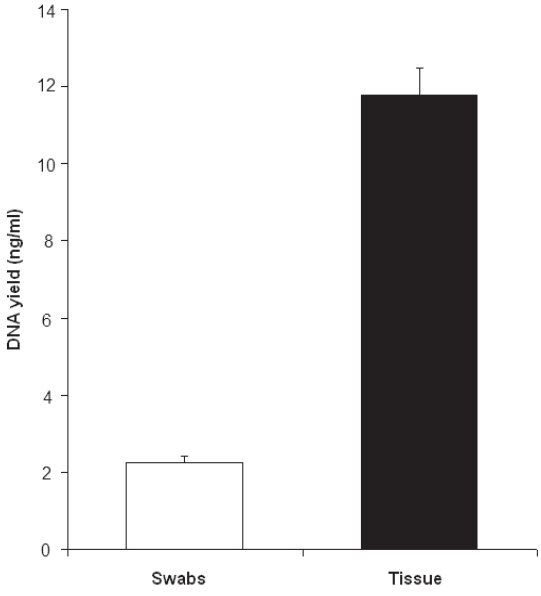


Figure 1: Total DNA yield (ng/ml) for buccal swab sampling and tissue sampling for the same individuals (n = 49). Error bars are standard errors.

Table 1: Genotyping success, average peak heights and number of unspecific peaks in swab and tissue samples (n = 49).

	swabs (diluted 1:10)	tissue (diluted 1:10)
primer C8		
number of genotyping failures	12	15
average peak height	1285.1 ± 211.5	904.5 ± 161.6
number of unspecific peaks	11	45
primer B4		
number of genotyping failures	7	5
average peak height	3273.9 ± 510.9	5828.1 ± 648
number of unspecific peaks	2	7

We found a significant interaction between sampling method and DNA yield on peak height (ANCOVA, $F_{1,148} = 8.0$, $p = 0.005$). As peak heights differed significantly between loci (ANCOVA, $F_{1,148} = 56.3$, $p < 0.001$) and sampling method ($F_{1,148} = 7.45$, $p = 0.007$), we analysed each locus and method separately. Peaks of tissue samples were significantly higher than peaks of buccal swabs for locus B4 (paired t-test, df = 38, t = 3.3, $p = 0.002$), but not for locus C8 (paired t-test, df = 24, t = 0.95, $p = 0.35$). Peak heights differed significantly between loci for both swab samples (paired t-test, df = 35, t = 3.7, $p < 0.001$) and tissue samples (paired t-test, df = 28, t = 6.2, $p < 0.001$). The number of unspecific peaks was significantly higher for locus C8 than for B4 (Fishers Exact-test; $\chi^2 = 17.3$,, df = 1, $p < 0.001$, Fig. 2). Unspecific peaks occurred significantly more often in tissue samples than in swab samples for primer C8 (χ^2-test, $\chi^2 = 12.1$, df = 1, p-value < 0.001), but not for primer B4 (Fishers Exact-test, χ^2-test, $\chi^2 = 0.62$, df = 1, $p = 0.43$, Fig. 2).

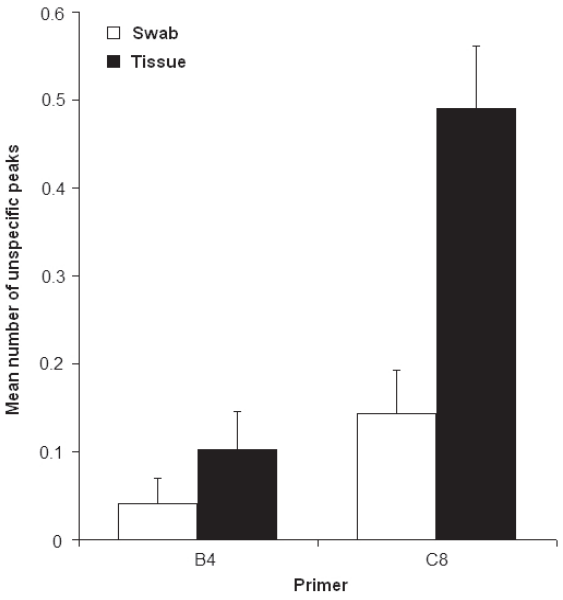


Figure 2: Mean number of unspecific peaks between loci and between swab and tissue samples (n = 49, respectively). Error bars are standard errors.

In the swab data, we found a significant positive correlation between peak height and DNA yield for both loci (linear regression, B4: $p = 0.001$, $R^2 = 0.23$; C8: $p = 0.04$, $R^2 = 0.11$). This correlation was most obvious in the lower range of yield of DNA up to 3 ng/ml (Fig. 3). Large peak heights were already reached at 2 ng/ml. At 3-5 ng/ml DNA yield, peak heights were not increasing anymore. Peak heights < 40 were not distinguishable from background noise. For tissue samples, no significant correlation between peak height and DNA yield was found. The yield of DNA was not significantly correlated with amplification failures (ANOVA, $F_{1,192} = 0.24$, $p = 0.62$). We did not found a lower threshold of DNA yield for successful amplification, as even the lowest DNA yield (0.097 ng/ml) generated genotypes.

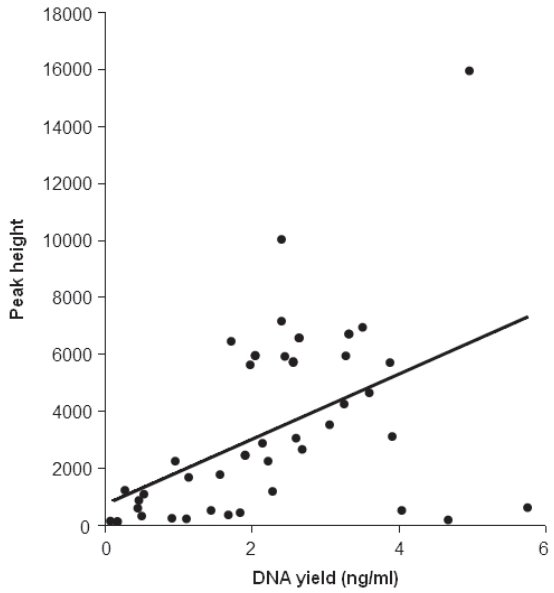


Figure 3: Correlation of DNA yield and peak height among swab samples for primer B4 (n = 49).

Occurrence of unspecific peaks was significantly correlated with the yield of DNA in tissue samples for primer C8 (Generalized Linear Model: df = 190, z = 2.15, p = 0.03). 57.7% of samples with a DNA yield > 10 ng/ml exhibited unspecific peaks, whereas only 22% of samples with a yield of DNA < 10 ng/ml exhibited unspecific peaks. Our results corroborate other studies in identifying buccal swabbing as a reliable non-invasive tissue sampling method for DNA analysis in reptiles (Miller 2006, Beebee 2008). Buccal swabs generated genotypes just as well as tissue samples. However, in contrast to Beebee (2008) the results obtained from swabs were not more reliable than those from tissue samples. Beebee (2008) suggested that the sampling technique of screwing tail tips might facilitate a higher probability in contamination of DNA in tissue samples. This can be avoided by a thorough and clean working procedure. Although the DNA yield from buccal swabs was much lower than from tissue, it was sufficient for a successful amplification. We did not find any lower threshold of DNA quantity that increased genotyping errors (Taberlet et al. 1999). In some cases the DNA yield from buccal swabs reached rather high values, but this was possibly caused by partial bleeding of some individuals. Interestingly, our results also show that very high DNA yields (>10 ng/ml), as found in some tissue samples, might be disadvantageous as they produce more unspecific peaks. In these cases, a dilution can help to optimize the results.

In conclusion, buccal swabs are a reliable non-invasive sampling method for DNA analysis in lacertid lizards that do not harm the specimens in their locomotory performance and energy reserves. Furthermore, this kind of sampling is probably less stressful for the species. However, patience and caution is needed to wait for the lizard to stop biting into the swab in order to preserve their teeth. It has to be mentioned that this sampling method can only be used for adult lizards with a minimum snout-vent length of 50mm, since even the smallest available swabs are too big for sampling smaller *P. muralis* without harming the individual. Whenever possible flexible dry swabs with a fine narrow bud, like the MW-100 swab (Medical Wire & Equipment) should be used, since buds of standard cotton swabs are too big for sampling. Apart from the primary concern of the animals' welfare, another advantage of buccal swabbing is the time-saving DNA extraction, since there is no need to remove scales, chop up the tissue and also not for a long digestion step. Moreover, the method will certainly help to convince nature conservation authorities that sampling for population genetic studies will not harm individuals in natural populations.

Acknowledgements

This work benefited from a grant of the 'Deutsche Bundesstiftung Umwelt' (DBU) (no.: 27282/33/2). We are grateful to Petra Willems for help in the laboratory. Permits for sampling wall lizards were obtained by the responsible administration of the federal state of Saxony.

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Chapter III

Geographic origin of a population of the Italian Wall Lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810), introduced north of the Alps

Schulte, U. & J. Gebhart (2011): Geographic origin of a population of the Italian Wall Lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810), introduced north of the Alps. – *Herpetozoa* 24(1/2): 96-97.

The Italian Wall Lizard *Podarcis siculus* (RAFINESQUE-SCHMALTZ, 1810), naturally occurs in the Appennine Peninsula, Sicily, Sardinia and Corsica, and along the northeast Adriatic coast. The lizard, however, was introduced to numerous locations in the Mediterranean region, where it established self-sustaining populations (Iberian Peninsula, Balearic Islands, France, Montenegro, Turkey, Libya, Tunisia.- PODNAR et al. 2005; ZAWADZKI & SEEMAN 2009). Additionally, introduced and established *P. siculus* populations are known from North American locations situated at about the same parallel of latitude as their Mediterranean conspecifics (Topeka, Kansas; Long Island, New York; Mt. Laurel, New Jersey; Los Angeles county, California.- BURKE & DEICHSEL 2010; DEICHSEL et al. 2010). The most thriving population extended its range around Long Island, New York, along power lines, railroads and by human-facilitated jump dispersal, over 30 miles, since its introduction in 1966, now reaching Manhattan and the Bronx (BURKE 2005). Contrary to its congener, the Common Wall Lizard *Podarcis muralis* (Laurenti, 1768), *P. siculus* generally failed to successfully colonize European regions outside its Mediterranean native range e.g., north of the Alps (SCHULTE et al. 2011). In Germany, the species was introduced around 1913 at the Schlossberg (castle hill) and river Dreisam in the town of Freiburg. However, the population became extinct here as a consequence of habitat destruction after roadwork or unfavourable climate conditions over a period of time in the early 1960s (TRAUTMANN 1924 in HENLE & FRITZ 2007). Also a population introduced to Offenburg must be considered extinct after a harsh winter in 1928/1929 (HENLE & FRITZ 2007). There are reports of introduced *P. siculus* of unknown fate from Basel, Remigen and Chiasso in Switzerland (HOHL 1985; KRAMER & STEMMLER 1988).

At present, the largest introduced population of *P. siculus* living north of the Alps is the population of Rapperswil, Switzerland (47.2274374°N, 8.8223648°E), where the first observation of *P. siculus* was close to the zoo in the vicinity of the local railway station and dates back to the 1980s (BILLING, pers. obs. in KLÖTZLI & ROSENMAYR 2000). In 1996, the latter authors assessed the population and estimated its size at about 70 individuals. The center of expansion of this population was the ruderal embankment of the south-exposed railway. Although it was impossible to closely examine the railway embankment due to a fence, the second author counted at least 28 individuals at the end of March 2011. Whether this population stems from an accidental introduction by cargo or an intentional, human-mediated introduction remains just as unknown as its ecological impact on the native communities of the Sand Lizard *Lacerta agilis* LINNAEUS, 1758. Based on morphological criteria, KLÖTZLI & ROSENMAYR (2000) suggested the specimens to belong to the subspecies *Podarcis siculus campestris* DE BETTA, 1857. In the present study, the origin of the population was identified by means of a roadkill (DOR) specimen that was collected there accidentally at a roadside ditch and preserved in 70% ethanol. DNA was extracted from muscle tissue of the tongue using the Qiagen® Dneasy® Blood & Tissue Kit (Qiagen®, Hilden) following the manufacturers' protocol. We sequenced a 656 bp fragment using the primers LGlulk (5'-AACCGCCTGTTGTCTTCAACTA-3') and HPod (3'-GGTGGAATGGGATTTTGTCTG-5') (PODNAR et al. 2007; see SCHULTE et al. 2011). Sequencing was performed with the DYEnamic™ ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich) for sequencing reactions run on a

MegaBACE 1000 automated sequencer. The DNA sequence was corrected and aligned by eye. For lineage assignment, the sequence was aligned to sequences from individuals sampled within the entire native range of *P. siculus* provided by PODNAR et al. (2005).

Fig. 1: *Podarcis siculus campestris* DE BETTA, 1857, male from Rapperswil, Switzerland.

The analyzed specimen clearly belonged to the "Po plain group" within the *campestris-siculus* haploclade (PODNAR et al. 2005) and differed in only two substitutions from this haplotype. This subclade can be found in the Po plain (Italy) and the northern Adriatic region (Croatia) and forms the species' northern range border. The subclade does not trespass the Alps, which act as a natural topographical and possibly also a climatic barrier. The climate conditions prevailing in this subclade's range area and at the novel locality in Switzerland seem to overlap. Hence, it is likely that this clade might have been pre-adapted to the environmental conditions in Switzerland, like it is the case with its congener *P. muralis*, where those clades that most frequently colonized Central Europe are the northernmost clades (Southern Alps and Eastern France Clades.- SCHULTE et al. 2011).

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Chapter IV

Origin and genetic diversity of an introduced wall lizard population and its cryptic congener

Schulte, U., Gassert, F., Geniez, P., Veith, M. & A. Hochkirch (2012): Origin and genetic diversity of an introduced wall lizard population and its cryptic congener. – *Amphibia-Reptilia* 33: 129-140.

Abstract: The Common Wall Lizard (*Podarcis muralis*) has been introduced within large parts of Central Europe, the UK and parts of North America. In an introduced population of this species in Lower Saxony, Germany, we found in addition to mtDNA haplotypes of *P. muralis* also haplotypes of its congener *Podarcis liolepis*, a species that hitherto has never been recorded outside its native range. We therefore, (1) wanted to identify the geographic origin of the founder individuals of both non-native populations, (2) test for hybridization between introduced individuals of both species in Germany and (3) compare levels of genetic diversity between native and introduced populations. We sequenced a fragment of the mitochondrial cytochrome *b* gene and genotyped individuals of the introduced as well as native populations of both species at eleven microsatellite loci. Our results suggest that the founders presumably stem from a region in the eastern Pyrenees, where sympatric populations of *P. muralis* and *P. liolepis* are known. No evidence for gene flow between the two species was found in the introduced population. These results are consistent with behavioural observations indicating agonistic interactions of *P. muralis* towards *P. liolepis* rather than cross-species attraction. Compared to the native populations, high levels of genetic diversity have been retained in the introduced population of both species and no evidence for a genetic bottleneck was found. The effective population size was high in *P. muralis*, but substantially smaller in *P. liolepis*.

Key words: invasive species, effective population size, genetic variability, bottleneck effect, hybridization, microsatellite, mtDNA.

Introduction

Globalization has favoured an exponential increase in the rate and spatial extent of alien species introductions worldwide. The ecological threat posed by alien invasive species is a severe problem in nature conservation (Strayer et al., 2006; Perrings et al., 2010). During recent decades, a considerable amount of research has been carried out to study contemporary evolutionary events in the process of biological invasions in order to determine which mechanisms drive invasions and to evaluate the impact of invasions. It is generally believed that genetic attributes like additive genetic variance, epistasis, heterosis, genetic drift and genomic rearrangements promote the success of invaders as they provide a buffer to respond to natural selection and allow adapting to new environments (reviewed in Lee, 2002). Several recent studies have shown that invasive populations often exhibit only minimal reductions in genetic diversity as a consequence of a large number of founders or multiple introductions (Holsbeek et al., 2008; Simberloff, 2009). Furthermore, admixture of genotypes from different source populations often boosts genetic diversity and therefore, may support the invasiveness of species (Kolbe et al., 2004; Pairon et al., 2010). As a consequence of genetic drift, selection and hybridization, a rapid genetic divergence of invasive populations from their ancestral source population is often observed (Bossdorf et al., 2005).

Due to the inevitable bias of nearly exclusively sampling successful invasive populations, a loss of genetic diversity associated with population bottlenecks during the invasion processes is reported less frequently (Kelly et al., 2006). In general, a loss of genetic diversity occurs in introduced populations that have been founded by a few closely related individuals, which only represent a subset of the genetic variability of a certain source population within the native range (so called founder effect). Although many studies found patterns of inbreeding and outbreeding in invasive populations (e.g. Huxel, 1999; Facon et al., 2011), a small number of founders, high inbreeding and low genetic variation does not necessarily lead to negative fitness consequences or extinction of invasive populations (Verhoeven et al., 2011).

The Common Wall Lizard (*Podarcis muralis*) is one of the few reptile species that has successfully colonized regions in north-western Europe and North America far outside its sub-Mediterranean native range. While determining the origin of 77 introduced wall lizard populations in Central Europe, we discovered one mitochondrial haplotype of the Catalonian wall lizard (*Podarcis liolepis*) at one location (Nörten-Hardenberg, Germany) together with two haplotypes of the Western France *P. muralis* Clade (see fig. 1; Schulte et al., 2012). Based upon information of local residents, the population stems from an intentional introduction and exist at least since the end of the 1980s (Schulte et al. 2011). Recently considered as a valid species within the *P. hispanicus* complex (Renoult et al., 2009; Renoult et al., 2010), *Podarcis liolepis* is distributed in the northern Iberian Peninsula (Catalonia, the Ebro Valley, Basque Country, the northern Castilian Plateau southwards to Valencia) and in southern France up to the Rhone river (Carretero, Marcos and de Prado, 2006; Renoult et al., 2010; Kaliontzopoulou et al., 2011; fig. 2). Morphologically, *P. muralis* and *P. liolepis* are relatively difficult to

distinguish (Gosá, 1985; Pérez-Mellado, 1998; Vacher and Geniez, 2010). Introduced populations might thus be overlooked, particularly as the latter species is usually not expected outside its native range.

In order to gain a deeper understanding of the rapid parallel establishment of these two non-native wall lizards at a single locality in Germany, we focused on their genetic architecture by using a combination of phylogeographic marker systems (mtDNA) and highly variable microsatellite markers. We specifically wanted to (1) identify the putative source region of the introduced populations of both species, (2) test for hybridization between introduced individuals of both species in Nörten-Hardenberg (Germany) and (3) compare levels of genetic diversity between native and introduced populations.

Figure 1. Lateral view of a male specimen (NOE14) from Nörten-Hardenberg (Germany) attributed to *Podarcis liolepis liolepis*. Photo: US (16.06.2010).

Materials and methods

Sampling

A total of 51 lizards (juveniles and adults of both sexes) were captured by hand or by noosing randomly from the introduced mixed population in Nörten-Hardenberg in July 2010 (Lower Saxony, Germany, fig. 1/2). Lizards autotomized the tail tip after exerting light pressure and were immediately released afterwards. Tail tips were stored in 99.8% ethanol p.a. Additionally, 15 individuals were sampled at a locality in Labeaume (Département Ardèche, Southern France), where *P. muralis* and *P. liolepis* also occur in syntopy. We added 25 samples of *P. muralis* from Montségur (n = 13; Département Ariège), Lourdes (n = 6; Département Hautes-Pyrénées) and La Rochelle (n = 6; Département Charente-Maritime). For the mtDNA analyses we used samples of *P. muralis* from Amboise and Saint-Malo as well as a museum specimen of *P. liolepis* from Planoles (Spain, fig. 2).

Assignment of geographic origin

Sequence data were collected for ten morphologically variable specimens from the introduced German population, for ten samples from six native French populations (Labeaume, Montségur, Lourdes, La Rochelle, Amboise and Saint-Malo) and for one specimen from Planoles (Spain) (fig. 2). DNA was extracted from muscle tissue of autotomized tail tips or of the tongue (museum specimens) using the QIAGEN DNEasy Blood and Tissue Kit (QIAGEN, Hilden) following the manufacturers' protocol. For amplifications of cytochrome *b* PCR fragments we used 50 μl reaction tubes containing: 27 μl purified water, 20 μl of *Taq* polymerase (QIAGEN Hotstar), 1 μl of each PCR primer and 1 μl of genomic DNA. Reaction conditions comprised an initial denaturation step for 15 min at 95°C, 35 cycles of 30 s at 94°C, 30 s at 43°C, 90 s at 72°C, and a final extension step of 10 min at 72°C. We sequenced a 656- to 887-bp fragment of the mitochondrial cytochrome *b* gene using the primers LGlulk (5'-AACCGCC TGTTGTCTTCAACTA-3'), Sicnt (5'-TTTGGATCCCTGTTAGGCCTCTGTT-3') and HPod (3'-GGTG GAATGGGATTTTGTCTG-5') (Podnar et al., 2007; Schulte et al., 2012). Sequencing was performed with the DYEnamic ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich) for sequencing reactions run on a MegaBACE 1000 automated sequencer. DNA sequences were corrected and aligned by eye. Sequences were deposited in GenBank under the accession numbers JQ403287-JQ403304. For lineage assignment, the sequences were aligned to sequences from individuals sampled within the native range of *P. muralis* (Carranza, Arnold and Amat, 2004; Busack, Lawson and Arjo, 2005; Giovannotti, Nisi-Cerioni and Caputo, 2010) or within the invasive range, when the geographic origin of the introduced population was known (see Schulte et al., 2012). Therefore, we included twelve *P. muralis* sequences of a preliminary study (Schulte et al. 2012) representing six different genetic lineages of the species which have been introduced in Germany. Sequences of the *Podarcis hispanicus* species complex, including seven of *P. liolepis* from Tarragona, Barcelona, Girona, the Pyrenees, Burgos and Medinaceli (Castilla y León) , one of *Podarcis vaucheri* from Morocco, one of *P. hispanicus* sensu stricto from Valencia as well as one sequence of *Podarcis siculus* as outgroup were obtained from GenBank (AF052633, AF052635; Castilla et al., 1998; AF469432, AF469434, AF469436, AF469438, AF469440, AF469442, Harris and Sá-Sousa, 2002; DQ081144; Pinho, Ferrand and Harris, 2006; FJ867396, Giovannotti, Nisi-Cerioni and Caputo, 2010; see fig. 2 and 3). As we focused on detecting the geographic origin within the native ranges of *P. liolepis* and *P. muralis* (Western France Clade), we ignored additional sequences from other Spanish lineages or species (Kaliontzopoulou et al., 2011). In order to assign introduced haplotypes to intraspecific evolutionary lineages of *P. muralis* and *P. liolepis* and their respective geographic range via a phylogenetic tree, we used Bayesian inference in MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). We applied the best-fit substitution model (GTR+I+G) suggested by MrModeltest 2.2 (Nylander, 2004). We ran four Monte Carlo Markov chains for one million generations each and sampled a tree every 100 generations. This was sufficient to let the average standard deviation drop below 0.01. We discarded 2500 trees as burn-in after checking for stationary and convergence of the

chains. Support of the nodes was assessed with the posterior probabilities of reconstructed clades as estimated in MrBayes (Ronquist and Huelsenbeck, 2003).

Genotyping

We genotyped 51 individuals of the introduced wall lizard population, 14 individuals of the native *Podarcis liolepis* population from Labeaume and 25 *P. muralis* individuals from three native populations in south-western France. All individuals were genotyped at eleven microsatellite loci, six of which have been developed for *Podarcis muralis* (A7, B3, B4, B7, C8, C9; Nembrini and Oppliger, 2003), two for *Zootoca vivipara* (Lv-4-alpha, Lv-472, Boudjemadi et al., 1999) and three for *Podarcis bocagei* (Pb10, Pb50, Pb73; Pinho et al., 2004). Amplification was performed in a Multigene Gradient Thermal Cycler (Labnet) using the 2.5 x 5PRIME HotMasterMix (5PRIME). For each PCR we used 5 μl reaction mix containing: 1.2 μl genomic DNA, 2.2 μl HotMasterMix, 2.2 μl water and 0.1 μl of the forward and reverse primers. The PCR conditions were as recommended by the manufacturer, with locus-specific annealing temperature between 53°C and 61°C. The 5'-end of each forward primer was labelled with a fluorescent dye, either FAM, TAMRA or HEX. PCR products were run on a MegaBACE 1000 automated sequencer. Fragment lengths were determined using MegaBACE ET550-R size standard and MegaBACE Fragment Profiler (Amersham Biosciences).

Data analysis and descriptive statistics

We tested our data for the occurrence of null alleles with MICRO-CHECKER 2.2.3 (Van Oosterhout et al., 2004) and for linkage disequilibrium with Fstat 2.9.3.2 (Goudet, 2001). STRUCTURE 2.3.3 (Pritchard, Stephens and Donnelly, 2000) was used to analyse for genetic structuring among subpopulations. The admixture model was used as we wanted to test for potential hybridization. We chose the correlated allele frequency model with a burn-in of 100000 simulations followed by one million Markov chain Monte Carlo simulations. Tests were run for K = 1-10 with ten iterations per K. This range of values for K was chosen taken into consideration that we have sampled four *P. muralis* populations and two *P. liolepis* populations. Several methods have been proposed to infer the optimal K value from STRUCTURE runs. The method described by Pritchard, Stephens and Donnelly (2000) is known to sometimes lead to asymptotic convergence and tends to result in too high K values. The optimal K value suggested by Evanno, Regnaut and Goudet (2005) is based on the second order rate of change (ΔK) and tends to result in low K values (Hausdorf and Hennig, 2010; Campana et al., 2011). Recently, a new method (ΔF_{ST}) has been proposed by Campana et al. (2011). We compared all three methods in the CorrSieve package for R (Campana et al. 2011). However, based upon our sampling design, we expected that a biologically meaningful minimum value for K would be four (as we sampled two species and each from at least two very distant localities). The results obtained using ΔF_{ST} (K = 2) and ΔK (K = 3) both suggested values that appeared not biological meaningful. We suppose that this is caused by the strong differentiation at the species level. As our ln$P$(D) values showed no asymptotic convergence and K was

biological meaningful, we used the K value with the highest average ln$P$(D) value as suggested by Pritchard, Stephens and Donnelly (2000).

We used GenAlEx 6.4.1 (updated from Peakall and Smouse, 2006) to calculate the number of alleles (N_A), the inbreeding coefficient (F_{IS}), as well as for expected and observed heterozygosities (H_E and H_O) for each locus and population. Fstat was used to calculate allelic richness (A_R). As traditional methods of population differentiation (F_{ST}, G_{ST}) have recently been strongly criticized, we calculated D_{EST} as an estimate of population differentiation (e.g. Jost, 2008; Gerlach et al., 2010) using the DEMEtics package for R (Gerlach et al., 2010). However, in our case F_{ST} and D_{EST} had a strong linear correlation (R^2 = 0.91). Therefore, we used F_{ST} in an AMOVA with 9999 iterations in GenAlEx with the genetic clusters suggested by STRUCTURE as populations and the two species as "regions". We estimated the effective population size (N_E) of clusters identified by STRUCTURE using ONeSAMP, which uses an approximate Bayesian computation for estimating N_E and 95% confidence limits (CL) (Tallmon et al., 2008). The program generates 50000 simulated populations with N_E between a conservatively estimated lower and upper bound for N_E (for all four populations: 2-500). After executing ten iterations of estimating N_E we calculated the mean and standard deviation of N_E for each population.

To detect recent bottlenecks in the introduced populations, the program BOTTLENECK 1.2.02 was used (Cornuet and Luikart, 1996). Recent bottlenecks (0.2 – 4 N_E generations) can create a heterozygosity excess compared to populations at mutation-drift equilibrium, because rare alleles that have little impact on heterozygosity can be lost quickly. We calculated H_{EQ} using the two-phase model with a variance of 30 and a proportion of 70% of the step-wise mutation model in the two-phase model (Di Rienzo et al., 1994), as this is believed to be the most likely mutation model for microsatellites (Piry, Luikart and Cornuet, 1999). Statistical significance was assessed with a one-tailed Wilcoxon-test, since this test proved to be the best for less than 20 loci (Piry, Luikart and Cornuet, 1999). Analyses were performed with 1000 iterations.

Results

Geographic origin of the introduced populations

The introduced population of *P. muralis* in Nörten-Hardenberg belongs to the Western France mtDNA clade (fig. 3). This lineage differs substantially from seven other introduced *P. muralis* lineages found in Central Europe (Schulte et al., 2012), with an average p-distance of 0.049 to its sister clade (Eastern France clade). Three of four individuals shared one haplotype, while the fourth individual had a very similar haplotype (p-distance of 0.002). These haplotypes were most similar to haplotypes found in Andorra and Benasque (Carranza, Arnold and Amat, 2004; Busack, Lawson and Arjo, 2005) and differed substantially from another introduced population of this lineage in Germany (Mainz), which originated from the Atlantic coast of southern France. Therefore, the *P. muralis* population in Nörten-Hardenberg

most probably originated from a region in the eastern Pyrenees. Six haplotypes that differed in two substitutions were found among the introduced *P. liolepis* individuals.

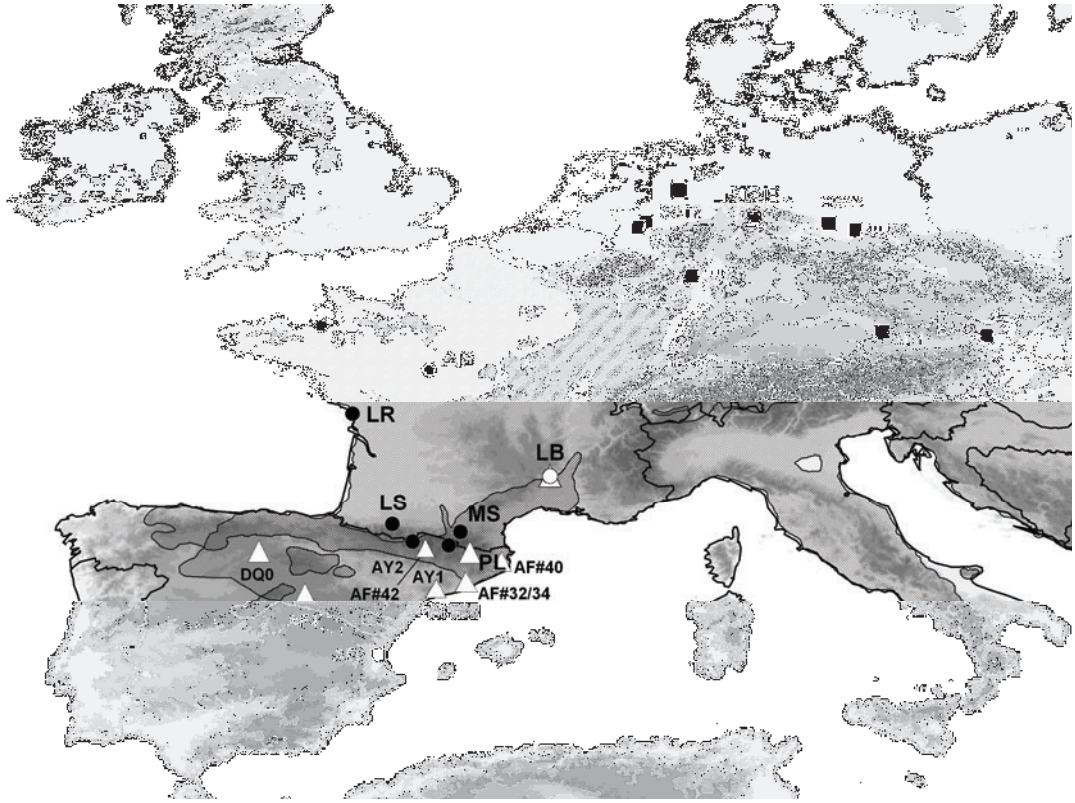

Figure 2. Location of the introduced population in Germany (NOE, Nörten-Hardenberg, Lower Saxony) and geographic range of *P. liolepis* (upward diagonal shaded area, from Renoult et al. 2010 and Kaliontzopoulou et al. 2011) and *P. muralis* (downward diagonal shaded area, from Schulte 2008) in western Europe. Sampled localities within the native ranges correspond to symbols (black dots: *P. muralis* Western France Clade; white triangles: *P. liolepis*; white square: *P. hispanicus* sensu stricto). Black squares within Germany and Austria correspond to introduced *P. muralis* populations representing six different genetic lineages (see Appendix S1): BR1 = Bramsche; BOT2 = Bottrop; UU60 = Duisburg-Hüttenheim; UU70 = Mainz; NOE, Nörten-Hardenberg; HAN1 = Halle a. d. Saale; UU89 = Altenhain; SD1 = Schärding; BA18 = Klosterneuburg; LB, Labeaume; AM, Amboise; ST, St. Malo; LR, La Rochelle; LS, Lourdes; AY2, Benasque (AY234155); AF#42, Pyrenees (AF469442); AY1, Andorra (AY151908); MS, Montségur; PL, Planoles; AF#40, Girona (AF469440); AF#32/34, Barcelona (AF469432, AF469434); AF#38, Tarragona (AF469438); AF0, Valencia (AF052635, AF4, Medinaceli (AF469436) and DQ0, Burgos (DQ08114).

These haplotypes confirmed an affiliation to the subspecies *P. l. liolepis* (Boulenger, 1905), which occurs at the north-eastern coast of Spain, in the Central and East Pyrenees as well as in departments Pyrenées-Orientales, parts of Aude and occasionally in Haute-Garonne (Geniez and Deso, 2009). In the phylogenetic tree the haplotypes from the introduced population form a strongly supported group with the haplotype from Planoles in the province of Girona (fig. 3, p-distance: 0.01). The haplotypes of *P. liolepis* from the native population sampled in France (Labeaume) were rather different from the introduced clade (p-distance: 0.038) and confirmed an affiliation to the subspecies *P. l. cebennensis* (Guillaume and Geniez, 1986), which occurs in south-western France up to the departments Drôme and Vaucluse east of the river Rhone (Geniez et al., 2008). One haplotype from Labeaume represented the Eastern France Clade of *P. muralis* (fig. 3).

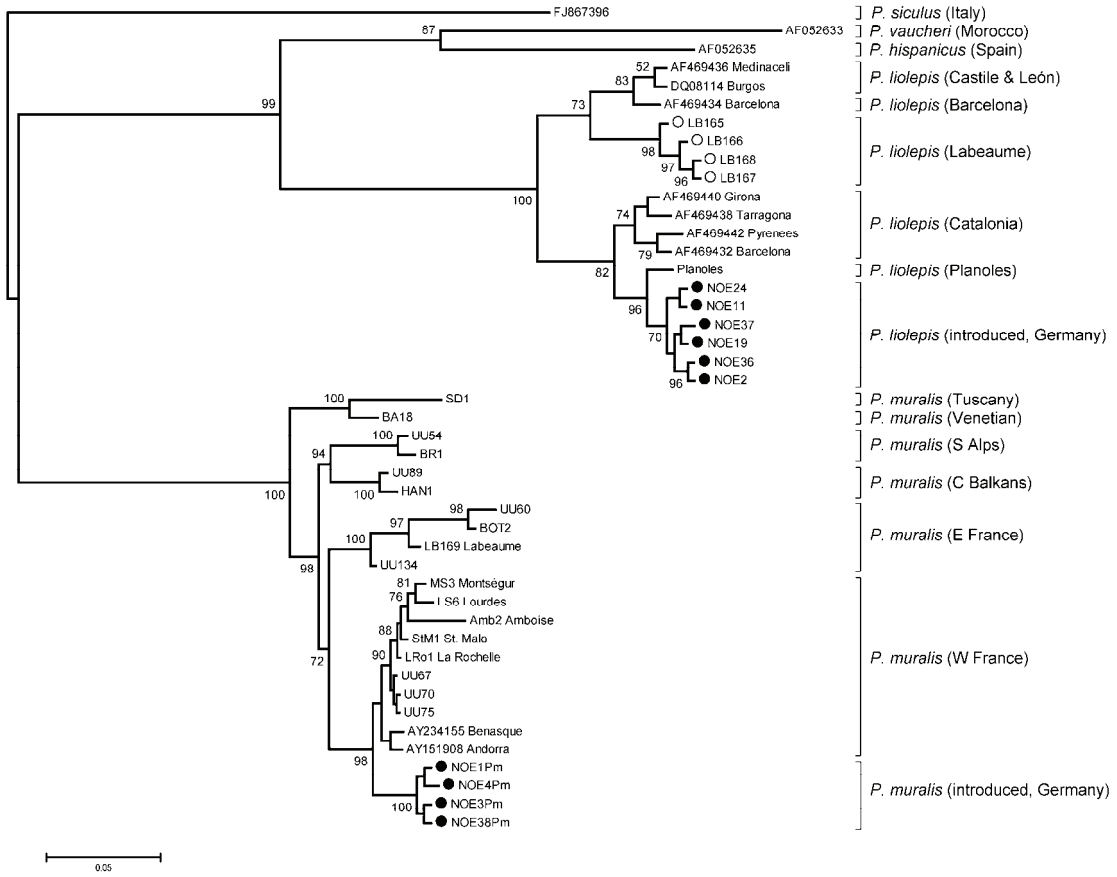

Figure 3. Bayesian consensus tree for the mitochondrial cytB gene for *Podarcis muralis* and *Podarcis liolepis*. Numbers are posterior probabilities. Filled circles represent samples from introduced populations in Nörten-Hardenberg (Lower Saxony, Germany), open circles represent *P. liolepis* samples from the native population in Labeaume (France) (for population names see Appendix S1).

Genetic structure

All microsatellite markers proved to be polymorphic for both species. We found evidence for null alleles at locus B3 in all populations and, therefore, excluded this locus from further analyses. There was no evidence for large allele drop-out or other scoring errors. All pairwise tests for linkage disequilibrium were non-significant ($p > 0.05$). The most likely number of genetic clusters (K) among all analysed populations revealed by model-based clustering in STRUCTURE was five (fig. 4). There was no indication for hybridization between both species at lower numbers of genetic clusters. If a higher K was chosen, likelihood values decreased and new genetic clusters appeared with no individual having a high probability (using a strict threshold value of $q = 0.20$) of belonging to it.

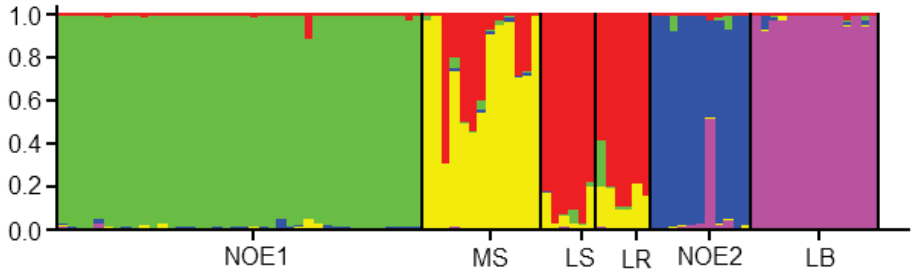

Figure 4. Genetic clusters obtained from the STRUCTURE analysis (K = 5) for all 90 samples. Each individual is represented by a single vertical line, divided into K colours. The coloured segment shows the individual's estimated proportion of membership to that genetic cluster. NOE1: *P. muralis*, introduced (Nörten-Hardenberg), MS: *P. muralis*, native (Montségur), LS: *P. muralis*, native (Lourdes), LR: *P. muralis*, native (La Rochelle), NOE2: *P. liolepis*, introduced (Nörten-Hardenberg), LB: *P. liolepis*, native (Labeaume).

A clear separation of the introduced and native *P. liolepis* population as well as between the native and introduced *P. muralis* population was found. This result was confirmed by the AMOVA, which revealed that a significant portion ($p < 0.001$) of the genetic variation was explained by "species" (16%) and "populations" (11%). Differentiation between native and introduced populations was high and only exceeded by differentiation among species (table 1). The lowest D_{EST} and F_{ST} values were found between the two native populations of *P. muralis*.

Table 1. Pairwise D_{EST} values (upper right part) and pairwise F_{ST} values (lower left part) between the native and introduced populations of *Podarcis muralis* and *Podarcis liolepis*. Population names: NOE, Nörten-Hardenberg; LB, Labeaume; LR, La Rochelle; LS, Lourdes; MS, Montségur.

	P. muralis (NOE, introduced)	*P. muralis* (LS/LR, native)	*P. muralis* (MS, native)	*P. liolepis* (NOE, introduced)	*P. liolepis* (LB, native)
P. muralis (NOE, introduced)		0.496	0.374	0.797	0.768
P. muralis (LS/LR, native)	0.142		0.131	0.771	0.669
P. muralis (MS, native)	0.098	0.048		0.780	0.680
P. liolepis (NOE, introduced)	0.268	0.268	0.263		0.496
P. liolepis (LB, native)	0.287	0.287	0.276	0.179	

Genetic diversity between native and introduced populations

Compared to the native populations of *P. muralis*, the introduced population had a lower allelic richness, but rather similar values of H_E and H_O (table 2). On the contrary, the introduced *P. liolepis* population had a higher allelic richness and expected heterozygosity than the native population. Only H_O was higher in the native than in the introduced population. Within the introduced populations, *P. muralis* had higher H_E and H_O values than *P. liolepis* (table 2). Native *P. liolepis* from southern France had the lowest H_E and H_O. The inbreeding coefficient (F_{IS}) was highest in the introduced *P. liolepis* population and lowest in the native *P. muralis* population from Montségur (table 2). Nevertheless, the introduced *P. liolepis* population exhibited a high genetic diversity.

Table 2. Comparison of genetic variability and effective population size (N_E) in introduced and native populations of *Podarcis muralis* and *Podarcis liolepis*; with *n* = number of samples, N_A = mean number of alleles, A_R = allelic richness, H_O and H_E = observed and expected heterozygosity, F_{IS} = inbreeding coefficient. Population names: NOE, Nörten-Hardenberg; LB, Labeaume; LR, La Rochelle; LS, Lourdes; MS, Montségur.

	n	N_E	N_a	A_R	H_O	H_E	F_{IS}
Podarcis muralis (NOE,introduced)	40	89 ± 13.35	9	6.43	0.691	0.685	0.042
Podarcis muralis (LS/LR, native)	12	25 ± 3.4	6.9	6.72	0.695	0.668	-0.042
Podarcis muralis (MS, native)	13	32 ± 2	7.2	6.73	0.708	0.658	-0.081
Podarcis liolepis (NOE, introduced)	11	23 ± 3.69	6.6	6.70	0.564	0.648	0.138
Podarcis liolepis (LB, native)	14	30 ± 2.69	6	5.95	0.621	0.601	-0.029

The estimated N_E of the introduced *P. liolepis* was much smaller than that of the introduced *P. muralis* (23 ± 3.69 vs. 89 ± 13.35, table 2). Effective population size of the native *P. liolepis* population in Labeaume was 30 ± 2.69, whereas the native *P. muralis* populations had an estimated N_E of 32 ± 2 (Montségur) and 25 ± 3.4 (cluster Lourdes/La Rochelle, table 2). We found no evidence for a genetic bottleneck (heterozygote excess) in any of the analysed populations of either species. Neither of the introduced populations exhibited significant departures from Hardy-Weinberg equilibrium.

Discussion

Geographical origin of the introduced populations

Our results suggest that both non-native wall lizard species stem from a region in the eastern Pyrenees, where the native ranges of both species overlap (see fig. 2) and syntopic populations of *P. liolepis* and *P. muralis* are frequent (Geniez and Deso, 2009). Although the temporal course of introductions remains unknown, we hypothesize that both populations were introduced simultaneously, as it is rather unlikely that they have been transported two times independently from the same area to exactly the same locality in Germany. This represents the first record of the Catalonian wall lizard (*Podarcis liolepis*) as a non-native species in Germany. The pathway of the introduction remains unclear, but an intended introduction is most likely as more than 73% of all known introduced populations in Germany can be traced back to human-mediated introductions (Schulte et al. 2008, 2011). Based upon the information of local residents, the introduction took place at least in the 1980s.

Genetic structure and diversity within the native and invasive range

Even though the native *P. liolepis* population was not the source population of the introduced population in Nörten-Hardenberg and more populations need to be analysed for further comparisons, we compare both populations regarding their genetic diversity. The high allelic richness of the introduced *P. liolepis* population might be caused by its origin in the centre of the species' distribution (eastern Pyrenees), while the native *P. liolepis* population analysed occurs at the northern edge of the species' range in the

department Ardéche in France (fig. 2). A reduced genetic diversity at a species' northern range margin is rather typical due to smaller population sizes, partial isolation, stronger genetic drift and higher selection pressure (Hewitt, 2001; Böhme et al., 2007). The effective population size of *P. liolepis* was rather small, while N_E in the introduced *P. muralis* population even exceeded the values found in the native populations. This might have been caused either by different founder numbers, different time of introductions or by an initial decrease in population size in the introduced *P. liolepis* population.

Our observation of a reduced allelic richness, but similar heterozygosity in the introduced *P. muralis* population compared to the native populations from Western France is in line with the expectation that allelic richness is more strongly affected by genetic drift than heterozygosity (Amos and Balmford, 2001). Compared to the available literature on genetic diversity within native *P. muralis* populations in Central Europe (Gassert, 2005; Altherr, 2007), heterozygosity and allelic richness of the native and introduced *P. muralis* populations were rather high. The Montségur population is located in the south-western part of the range, where Pleistocene glacial refugia may have existed. This might explain, why the population has conserved a higher genetic diversity than populations further north, such as in Switzerland (Altherr, 2007; Blondel and Aronson, 2010). The high genetic diversity of the introduced population might also be influenced by its origin from a hotspot of genetic diversity. Compared to an introduced population in Cincinnati, Ohio (Lescano, 2010) and other introduced populations in Germany (Schulte et al., unpublished data), originating from northern Italy (a hotspot of genetic diversity for *P. muralis*) the genetic diversity of the introduced *P. muralis* population in Nörten-Hardenberg was much higher. We thus hypothesize that propagule pressure of both species must have been quite high, since no sign for a recent bottleneck was detected within the introduced populations. Indeed, introductions of numerous individuals might occur frequently among hobby herpetologists, as a high propagule size has for example been reported from a population in Linz (Austria, 130 introduced individuals; Schulte, 2008). It is possible that the high genetic diversity of both non-native populations has facilitated their establishment success. However, in Cincinnati *P. muralis* appears to be a successful colonizer despite originating from a small number of only twelve founders and multiple bottlenecks (Lescano, 2010). Inbreeding and a loss of genetic diversity, therefore, do not necessarily hamper the successful establishment and spread of introduced species (Lindholm et al., 2005; Schmid-Hempel et al., 2007; Ficetola, Bonin and Miaud, 2008).

Although Pinho, Harris and Ferrand (2008) suggested that *Podarcis* species take a long time of divergence to acquire complete reproductive isolation and detected gene flow between *P. muralis* and *P. liolepis*, we did not find evidence for hybridization among the introduced populations. In contrast, we observed occasionally aggressive and territorial interactions of both sexes of *P. muralis* towards *P. liolepis*, with matings occurring exclusively among conspecifics. Furthermore, we observed a microhabitat segregation between both species (*P. muralis*: widely distributed even within the moister talus, *P. liolepis*: restricted to vertical structures in rocky habitats with crevices), which is known from sympatric populations throughout the range (Salvador, 1986; Castilla and Bauwens, 1991; Martín-Vallejo

et al., 1995; Carretero, Marcos and de Prado, 2006). In a recent study, Gabirot et al. (2010) suggest that chemical cues may reduce the occurrence of hybridization even between the genetically more closely related species *P. liolepis* from Columbretes islands and *P. hispanicus* (morphotypes 1 or 2) from Madrid. Hence, olfactory traits might also act as premating barriers between *P. muralis* and *P. liolepis* and it is likely that premating barriers are well developed considering the divergence times and overlapping distribution of both species (fig. 2).

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Appendix: *Podarcis muralis* and *Podarcis liolepis* populations sampled and used from GenBank with information on sample ID, species and clade affiliation, sampling locality, GenBank accession number and references.

Sample ID	Species (clade affiliation)	Sampling locality	GenBank accession	Reference
NOE1	*P. muralis* (Western France Clade)	Nörten-Hardenberg	HQ652969	Schulte et al. 2012
NOE3	*P. muralis* (Western France Clade)	Nörten-Hardenberg	HQ652966	Schulte et al. 2012
NOE4	*P. muralis* (Western France Clade)	Nörten-Hardenberg	JQ403287	This study
NOE38	*P. muralis* (Western France Clade)	Nörten-Hardenberg	JQ403288	This study
LB169	*P. muralis* (Eastern France Clade)	Labeaume, France	JQ403289	This study
MS3	*P. muralis* (Western France Clade)	Montségur, France	JQ403290	This study
LS6	*P. muralis* (Western France Clade)	Lourdes, France	JQ403291	This study
LRo1	*P. muralis* (Western France Clade)	La Rochelle, France	JQ403292	This study
StM1	*P. muralis* (Western France Clade)	St. Malo, France	JQ403293	This study
Amb2	*P. muralis* (Western France Clade)	Amboise, France	JQ403294	This study
AY151908	*P. muralis* (Western France Clade)	Andorra	AY151908	Carranza et al. 2004
AY234155	*P. muralis* (Western France Clade)	Benasque, Spain	AY234155	Busack et al. 2005
BR1	*P. muralis* (Salps Clade)	Bramsche, Germany	HQ652960	Schulte et al. 2012
UU54	*P. muralis* (Salps Clade)	Bramsche, Germany	HQ652944	Schulte et al. 2012
HAN1	*P. muralis* (Central Balkan Clade)	Halle a. d. Saale, Germany	HQ652958	Schulte et al. 2012
UU89	*P. muralis* (Central Balkan Clade)	Altenhain, Germany	HQ652886	Schulte et al. 2012
UU60	*P. muralis* (Eastern France Clade)	Duisburg-Hüttenheim, Germany	HQ652880	Schulte et al. 2012
BOT2	*P. muralis* (Eastern France Clade)	Bottrop, Germany	HQ652955	Schulte et al. 2012
UU134	*P. muralis* (Eastern France Languedoc subclade)	Germany	HQ652908	Schulte et al. 2012
UU67	*P. muralis* (Western France Clade)	Mainz, Germany	HQ652893	Schulte et al. 2012
UU70	*P. muralis* (Western France Clade)	Mainz, Germany	HQ652894	Schulte et al. 2012
UU75	*P. muralis* (Western France Clade)	Mainz, Germany	HQ652896	Schulte et al. 2012
BA18	*P. muralis* (Venetian Clade)	Klosterneuburg, Austria	HQ652943	Schulte et al. 2012
SD1	*P. muralis* (Tuscany Clade)	Schärding, Austria	HQ652937	Schulte et al. 2012
NOE2	*P. liolepis*	Nörten-Hardenberg	HQ652946	Schulte et al. 2012
NOE11	*P. liolepis*	Nörten-Hardenberg	JQ403295	This study
NOE19	*P. liolepis*	Nörten-Hardenberg	JQ403296	This study
NOE24	*P. liolepis*	Nörten-Hardenberg	JQ403297	This study
NOE36	*P. liolepis*	Nörten-Hardenberg	JQ403298	This study
NOE37	*P. liolepis*	Nörten-Hardenberg	JQ403299	This study
Planoles	*P. liolepis*	Planoles, Spain	JQ403300	This study
LB165	*P. liolepis*	Labeaume, France	JQ403301	This study
LB166	*P. liolepis*	Labeaume, France	JQ403302	This study
LB167	*P. liolepis*	Labeaume, France	JQ403303	This study
LB168	*P. liolepis*	Labeaume, France	JQ403304	This study
AF469432	*P. liolepis*	Barcelona, Spain	AF469432	Harris and Sá-Sousa 2002
AF469434	*P. liolepis*	Barcelona, Spain	AF469434	Harris and Sá-Sousa 2002
AF469436	*P. liolepis*	Medinaceli, Spain	AF469436	Harris and Sá-Sousa 2002
AF469438	*P. liolepis*	Tarragona, Spain	AF469438	Harris and Sá-Sousa 2002
AF469440	*P. liolepis*	Girona, Spain	AF469440	Harris and Sá-Sousa 2002
AF469442	*P. liolepis*	Pyrenees, Spain	AF469442	Harris and Sá-Sousa 2002
DQ081144	*P. liolepis*	Burgos, Spain	DQ081144	Pinho et al. 2006
AF052635	*P. hispanicus* sensu stricto	Valencia, Spain	AF052635	Castilla et al. 1998
AF052633	*P. vaucheri*	Atlas, Maroc	AF052633	Castilla et al. 1998
FJ867396	*P. siculus* (outgroup)	Italy	FJ867396	Giovannotti et al. 2010

Chapter V

Rapid genetic assimilation of native wall lizard populations (*Podarcis muralis*) through extensive hybridization with introduced lineages

Schulte, U., Veith, M. & A. Hochkirch (in press): Rapid genetic assimilation of native wall lizard populations (*Podarcis muralis*) through extensive hybridization with introduced lineages. – *Molecular Ecology*, doi: 10.1111/j.1365-294X.2012.05693.x.

Abstract: The Common Wall Lizard (*Podarcis muralis*) has established more than 150 non-native populations in Central Europe, stemming from eight geographically distinct evolutionary lineages. While the majority of these introduced populations are found outside the native range, some of these populations also exist at the northern range margin in south-western Germany. In order to a) infer the level of hybridization in contact zones of alien and native lineages and b) compare the genetic diversity among purebred introduced, native and hybrid populations we used a combination of maternally inherited markers (mtDNA: cyt*b*) and Mendelian markers (microsatellites). Our results suggest a rapid genetic assimilation of native populations by strong introgression from introduced lineages. Discordant patterns of mtDNA and nDNA variation within hybrid populations may be explained by directed mate choice of females towards males of alien lineages. In contrast to previous studies we found a non-linear relationship between genetic diversity and admixture level. The genetic diversity of hybrid populations was substantially higher than in introduced and native populations belonging to a single lineage, but rapidly reaching a plateau of high genetic diversity at an admixture level of two. However, even introduced populations with low founder sizes and from one source population retained moderate levels of genetic diversity and no evidence for a genetic bottleneck was found. The extent of introgression and the dominance of alien haplotypes in mixed populations indicate that introductions of non-native lineages represent a serious threat to the genetic integrity of native populations due to the rapid creation of hybrid swarms.

Key words: Introgression, gene pool swamping, hybrid swarm, invasive species, mtDNA, microsatellites;

Introduction

The displacement of native biota by invasive taxa is a serious threat to biodiversity (Williamson 1997, Primack 2006). One important mechanism behind such displacement processes is reproductive interference, including hybridization (Rhymer & Simberloff 1996, Lee 2002, Gröning & Hochkirch 2008). For the native population, hybridization can have variable consequences ranging from negative fitness effects, such as the loss of locally adapted alleles, outbreeding depression and displacement by gene pool swamping (Arntzen & Thorpe 1999, Vorburger & Reyer 2003, Schmeller *et al*. 2007, Sacks *et al*. 2011, Hochkirch & Lemke 2011), to positive effects caused by hybrid vigour (Drake 2006, Fitzpatrick & Shaffer 2007, Pfennig 2007). While interspecific hybridization is often recognized as a threat to biota, interbreeding among subspecies or evolutionary lineages is less often seen as a threat to native species (Meyerson et al. 2010). Augmentation has even been successfully used to diminish negative effects from inbreeding in conservation management (e.g. Johnson et al. 2010).

However, in the context of biological invasions, both positive and negative fitness effects from hybridization are problematic. Positive fitness effects may enhance the invasiveness in terms of adaptive divergence through a creation of novel genotypes (Ellstrand & Schierenbeck 2000, Kolbe *et al*. 2004, Wolfe *et al*. 2007), whereas negative fitness effects may lead to outbreeding depression and thus threaten the native population (Huff *et al.* 2011). Furthermore, the displacement of the native gene pool by non-natives may lead to a loss of local adaptations and disruption of co-adapted gene-complexes (Allendorf *et al*. 2001). The displacement of the native gene pool ('gene pool swamping') is one of the most detrimental effects of hybridization (Avise *et al.* 1997, Riley *et al.* 2003, Hall *et al*. 2006). It is driven by asymmetric hybridization, which is caused by differences in population sizes or selective advantages of invaders, leading to differences in reproductive success (Wirtz 1999; Gröning & Hochkirch 2008). Hybridization also causes serious problems in conservation practice as it is complicated to develop useful management strategies for hybrids of endangered species (Allendorf *et al.* 2001). This is even more problematic in intraspecific hybridization events, as legislation is usually not differentiating between conspecific native and introduced evolutionary lineages (Schulte *et al*. 2011a).

The Common Wall Lizard (*Podarcis muralis*) has successfully colonized regions in north-western Europe far outside its sub-Mediterranean native range. More than 150 self-sustaining populations have emerged mainly from intended introductions (Schulte 2008). Introduced populations in Central Europe have been assigned to eight geographically distinct evolutionary lineages (Schulte *et al*. 2012a): 1) Western France clade (native range: W France and parts of the Pyrenees); 2) Eastern France clade (SE France to W Germany and S Netherlands); 3) Southern Alps clade (NW Italy, S Alps and Inn valley); 4) Venetian clade (NE Italy to NW Croatia); 5) Tuscany clade (Tuscany to N Campania); 6) Romagna clade (NE Apennine); 7) Marche clade (C Italy and W Istria); 8) Central Balkans clade (Balkan Peninsula to NE Austria). In addition to the introductions outside the native range, there is also an increasing detection of introduced populations at the northern range margin of the species. The high phenotypic variability of this species (Bellati *et al*. 2011) often hampers the detection of such introductions within the native range

and makes it nearly impossible to detect hybridization based on a morphological basis.

The wall lizard represents an excellent model species for the study of genetic consequences of biological invasions. Due to the distribution pattern of the wall lizard in Central Europe, three major population types can be compared: (1) Purebred native populations at the northern range margin, (2) purebred introduced populations outside the native range stemming from different source regions and, (3) mixed populations between native and introduced wall lizards. This situation allows assessing the extent of intraspecific hybridization in mixed populations. Therefore, we first used a mtDNA marker (cyt*b*) to infer the geographic origin of introduced lineages in purebred introduced populations and their frequency in mixed populations. Second, we analyzed the degree of differentiation among and within populations with different invasion histories (using 13 microsatellite loci) to test the hypothesis that populations stemming from similar source regions are less differentiated than those from different regions. Third, we wanted to examine whether admixture between non-native and native lineages occurs in mixed population. Finally, we tested the assumption that genetic diversity of introduced populations increases with the degree of admixture (Kolbe *et al.* 2008).

Methods

Sampling

A total of 566 lizards were captured by hand or by noosing from ten populations in Germany (Fig. 1): (I) Mixed populations (= with both native and non-native mtDNA lineages): Freiburg Dreisam (FRD, *N* = 52), Freiburg Messe (FRM, *N* = 22), Lörrach/Inzlingen (LÖR, INZ, WÖL, *N* = 85), Mannheim (MAN, *N* = 49). (II) Purebred introduced populations (= with only one non-native mtDNA lineage): Bramsche (BRA, *N* = 60), Nörten-Hardenberg (NÖR, *N* = 40), Dresden (DRE, *N* = 63), Schloß Holte-Stukenbrock (SCH, *N* = 64), Ammelshain (AMM, *N* = 81), (III) Purebred native population (= with only native mtDNA haplotypes): Wittlich (WIT, *N* = 50). For all mixed populations the occurrence of native Wall Lizard populations has been documented since the 19th century (Dürigen 1897, Tab. 1) and the introduction of alien individuals had been proven in a previous study except for FRM (Schulte *et al*. 2011a). The times of the first records of native and introduced wall lizards at the study sites are documented in table 1. The population FRM was monitored in 2000 without any observations or suspicion of alien individuals (Fritz & Laufer, pers. comm. 2011) and was originally included in this study as a reference for native populations of *P. muralis*. However, this population turned out to be a mixed population as well (see results).

We collected DNA by non-invasively buccal swabbing each specimen using a diagnostic fine-tip dry swab (Medical Wire & Equipment, MW-100) (Schulte *et al*. 2011b). Samples were stored in sterile tubes at -20°C until DNA extraction. DNA was extracted using the Qiagen DNEasy blood and tissue kit following the manufacturer's protocol (replacing ATL buffer by 400 µl PBS buffer as recommended in the supplementary protocol).

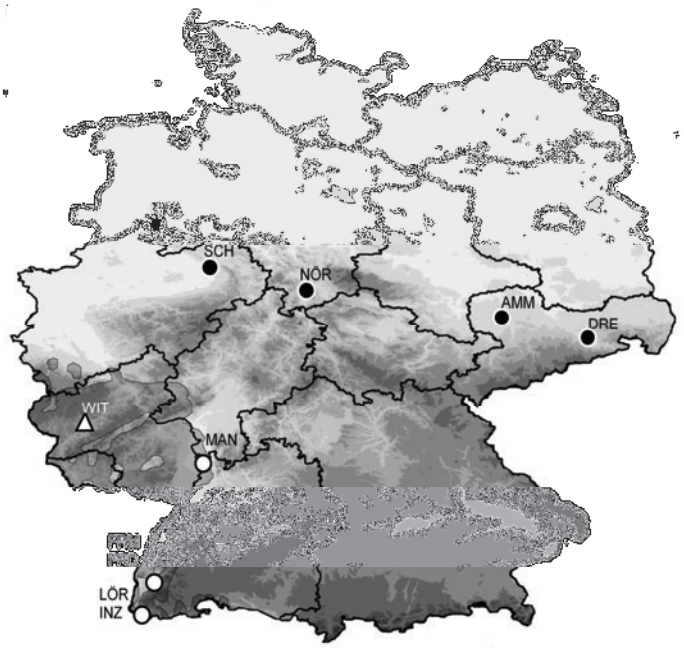

Fig. 1: Distribution of populations analysed in this study. White dots represent mixed populations, black dots represent purebred introduced populations and the white triangle corresponds to the native reference population (WIT). The shaded area in the Southwest shows the northern range margin of the Eastern France Clade of *P. muralis*.

Assignment of geographic origin

Sequence data were collected for all 208 specimens sampled in the four mixed populations as well as for some specimens in the purebred introduced and native populations (N = 22). For amplifications of cytochrome *b* fragments we used 50 µl reaction tubes containing: 27 µl purified water, 20 µl of HotStarTaq Master Mix (Qiagen Hotstar, including 0.4 U Taq polymerase, 90 mM KCl, 5 mM Mg^{2+}, 400 µM of each dNTP), 0.0625 pmol/µl of each primer and 2-10 ng of genomic DNA. Reaction conditions comprised an initial denaturation step for 15 min at 95°C, 35 cycles of 30 s at 94°C, 30 s at 43°C, 90 s at 72°C, and a final extension step of 10 min at 72°C. We sequenced a 656 bp mtDNA fragment (cyt*b*) using the primers LGlulk (5'-AACCGCCTGTTGTCTTCAACTA-3') and HPod (3'-GGTGGAATGGGATTTTGTCTG-5') (Podnar *et al.* 2007, Schulte *et al*. 2012a). The PCR product was purified using the High pure PCR product purification kit (Roche) according to the manufacturers' protocol. Sequencing reactions were performed using the DYEnamic ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich) and run on a MEGABACE 1000 automated sequencer. We corrected and aligned the sequences by eye. Ambiguous data from the beginnings and ends of the fragments were not included in the analyses. All sequences were deposited in GenBank under the accession numbers (JX065611-JX065629). For lineage assignment, the sequences were aligned with sequences from individuals with known origin (AY234155, Busack *et al*. 2005; DQ001023, DQ001024, DQ001028, DQ001029, DQ001032, Podnar *et al*. 2007; FJ867393, FJ867389, Giovannotti *et al*. 2010; HQ652963, HQ652952 (FRD); HQ652920, HQ652921 (LÖR); HQ652918, HQ652919 (INZ); HQ652960, HQ652874 (BRA); HQ652966, HQ652969 (NÖR); HQ652884 (DRE); HQ652905 (MAN); HQ652876, HQ652973 (SCH); HQ652885, HQ652886, HQ652887 (AMM), HQ652901, Schulte *et al*. 2012a, 2012b; Schweiger et al. unpublished data) and fitted into a phylogenetic tree using *P. siculus* and *P. melisellensis* as outgroups (HQ154646, AY185097, Podnar *et al*. 2004). We used Bayesian inference to infer a phylogeny as implemented in MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003), applying the parameters of

the substitution model (GTR+I+G) suggested by MrModeltest 2.2 (Nylander 2004). We ran the Monte Carlo Markov chain for two million generations, sampling every 2000 generations. We discarded 500 trees as burn-in after checking for stationary and convergence of the chains. Support of the nodes was assessed with the posterior probabilities of reconstructed clades as estimated in MrBayes (Ronquist & Huelsenbeck, 2003). This approach allowed us to assign introduced haplotypes to intraspecific evolutionary lineages of *P. muralis* and their respective geographic range (see also Schulte *et al*. 2012a). We used TCS 1.21 (Clement *et al.* 2000) and DnaSP 5 (Librado & Rozas 2009) in order to obtain haplotype frequencies.

Genotyping

All 566 individuals were genotyped at 13 microsatellite loci, seven of which were developed for *Podarcis muralis* (A7, B3, B4, B6, B7, C8, C9; Nembrini & Oppliger 2003), three for *Zootoca vivipara* (Lv-319, Lv-4-alpha, Lv-472, Boudjemadi *et al*. 1999) and three for *Podarcis bocagei* (Pb10, Pb50, Pb73; Pinho *et al.* 2004). Amplification was performed in a Multigene Gradient Thermal Cycler (Labnet) using the Qiagen Multiplex Mastermix or 5PRIME HotMasterMix. We used multiplexed PCR protocols for a combination of three or two loci with variable annealing temperatures (C9/B4/Pb73: 57°C; B3/Pb10/Lv319: 56°C; Lv472/Pb50: 53°C; A7/Lv4alpha: 60°C A7/B7: 60°C). Multiplex PCRs were performed in 10 µl reaction mix containing: 2-10 ng genomic DNA, 5.5 µl MultiplexMasterMix, 2.0 µl water and 0.1 µM of each primer. PCR conditions were used as recommended by the manufacturer. For primers C8 and B6 we used singleplex PCRs in a 5 µl reaction mix containing: 2-10 ng genomic DNA, 2.2 µl 5Prime MasterMix, 2.2 µl water and 0.0625 pmol of the forward and reverse primers at the locus-specific annealing temperature of 57°C. The 5'-end of each forward primer was labelled with a fluorescent dye, either FAM, TAMRA or HEX. PCR products were run on an MEGABACE 1000 automated sequencer. Fragment lengths were determined using Fragment Profiler 1.2 (Amersham Biosciences).

Population admixture analysis and descriptive statistics

As null alleles are often affecting microsatellite analyses, we tested our data in Micro-Checker 2.2.3 (Van Oosterhout et al. 2004) for the occurrence of null alleles. We used Fstat 2.9.3.2 to test for linkage disequilibria among loci (Goudet 2001), including also a test for linkage disequilibrium among mtDNA lineages and microsatellite genotypes. STRUCTURE 2.3.3 (Pritchard *et al*. 2000) was used to analyse for genetic structuring within and among populations. The admixture model was used, since it is more powerful in detecting potential hybridization. The admixture proportion of each individual *Q*, as an estimate of an individual's proportion of ancestry from each of the clusters, was obtained by STRUCTURE to separate hybrids from purebred parental individuals within populations (Vähä & Primmer 2006). We chose a conservative threshold value of Q = 0.20-0.80 for hybrid detection, since

values outside this range tended to detect hybrids even in purebred populations (see also Randi 2008, Sacks *et al*. 2011).

Within STRUCTURE we chose the correlated allele frequency model with a burn-in of 100,000 simulations followed by one million Markov chain Monte Carlo simulations. Tests were run for K = 1-15 with ten iterations per K. In order to find the optimal K value, we calculated the second order rate of change (ΔK) as suggested by Evanno *et al*. (2005) using the CorrSieve package for R 2.13 (Campana *et al*. 2011). Since the highest ΔK (at K = 12) suggested a finer population sub-structure in LÖR/INZ, we divided this population into three geographically defined sub-populations: LÖR, WÖL and INZ. As our sampling consisted of several levels of differentiation (distantly and closely related lineages, populations, hybrids within populations), we expected that ΔK would tend to find an optimal K between populations, but might fail to detect hybrids within populations, which might be part of such Hardy-Weinberg populations during a late stage of admixture. Therefore, we ran the analyses until the Q values for the next cluster dropped below 0.9 in all individuals (K = 15). We also performed STRUCTURE runs independently for single hybrid populations. The pattern of within-population structure of these runs for single populations remained identical compared to the complete dataset at K = 14.

In our special case, different time-scales (evolutionary lineages / populations) might play a role for population differentiation, making the choice of an ideal measure of differentiation difficult. R_{ST} (Slatkin 1991) might be an appropriate measure for the highly divergent evolutionary lineages in different non-native populations, as these lineages might have accumulated a high number of stepwise mutations during evolution. In contrast, F_{ST} might be more appropriate for population processes that have already reached Hardy-Weinberg-Equilibrium (Balloux & Lugon-Moulin 2002). On the other hand, the use of F_{ST} as a measure of population differentiation has recently been strongly criticized (e.g. Jost 2008, Gerlach *et al*. 2010). However, a recent analysis showed that F_{ST} performs well under certain conditions (Meirmans & Hedrick 2011). We, therefore, calculated in addition to F_{ST} also R_{ST} using GenAlEx 6.4 (updated from Peakall & Smouse 2006) and D_{EST} using the DEMEtics package for R (Gerlach *et al*. 2010). We ran a F_{ST}-based and a R_{ST}-based AMOVA with 9999 iterations in GenAlEx using the genetic clusters inferred according to the maximum ΔK in STRUCTURE.

We used Fstat to calculate the number of alleles (n_a), allelic richness (A_r) and the inbreeding coefficient (F_{IS}). Expected and observed heterozygosities (H_E and H_O) for each locus and population as well as deviations from Hardy-Weinberg-Equilibrium (HWE) were calculated in GenAlEx. We calculated an ANOVA in R 2.14.0 to test for significant differences in H_E between different admixture levels (i.e. number of lineages). In order to find an optimal function to describe the relationship between within-population genetic diversity (H_E) and the number of source populations (mtDNA clades), we used a curve fitting approach in Lab Fit 7.2.47 (Silva & Silva 2009).

In order to detect recent bottlenecks within introduced populations the program BOTTLENECK 1.2.02 was used with allele frequency data from a single temporal sample (Cornuet & Luikart 1996). Recent bottlenecks (0.2 – 4 N_E generations) can create a heterozygosity excess compared to populations at

mutation-drift equilibrium, because rare alleles that have little impact on heterozygosity can be lost quickly. We calculated H_{EQ} (expected heterozygosity corrected for sample size) using the two-phase mutation model (TPM, Di Rienzo *et al*. 1994), as this is the most likely mutation model for microsatellites (Piry *et al.* 1999). Statistical significance was assessed with a one-tailed Wilcoxon-test, since this test proved to be the best for microsatellite data with fewer than 20 loci (Piry *et al*. 1999). Analyses were performed with 1000 iterations.

Results

*Haplotype diversity (*mt*DNA)*

In total, we found 20 haplotypes belonging to seven different evolutionary lineages of *P. muralis* in our sample (Tab. 1, Fig. 2). The posterior probabilities of the lineages were high (≥ 99) and only some inter-nodes had a lower support. TCS obtained five non-connected haplotype networks with a maximum of six different haplotypes (Appendix S1). Although all mixed populations in southwestern Germany were located in the native range of the Eastern France clade, this lineage was completely missing in three populations (INZ, LÖR and MAN) and only one native haplotype was found in the FRD population. Even the FRM population, which was initially sampled as a native reference population turned out to contain only a small fraction of identical Eastern France haplotypes as in FRD (36%). Only in the WÖL population the native Eastern France haplotype dominated (95%). In INZ, LÖR and MAN, we found exclusively mtDNA lineages stemming from Italy (Tab. 1). Haplotype sharing among populations was relatively low, except for some adjacent populations (Appendix S1) and the Venetian haplotype, which was found in DRE, MAN and INZ. The highest non-native haplotype diversity was found for the Southern Alps lineage (six different haplotypes).

Genetic structure and differentiation

Within the populations INZ and LÖR we found no evidence for null alleles, whereas the other populations showed evidence for null alleles at 1-4 loci. However, no locus showed evidence for null alleles across all populations and nearly all Oosterhout values were below 0.2. Furthermore, in introduced populations deviations from Hardy-Weinberg-Equilibrium (HWE) may be caused by small founder sizes, increasing the rate of inbreeding. Hence, we did not exclude any locus from further analyses. All pair-wise tests for linkage disequilibrium were non-significant ($P > 0.05$). In some loci allele size ranges seemed to be specific for lineages. The locus A7 had two separate allele size ranges (152-200 and 390-412). The longer lengths were only found in populations with founders of the Venetian, Romagna and Tuscany clades.

Table 1. Native and non-native records of wall lizards within sampled populations (with information of number of founders and source region in some cases). Origin and genetic variability among mixed. purebred introduced and purebred native populations of *Podarcis muralis*; with mtDNA lineage frequency; Hapl.: recorded haplotypes; N = number of samples, n_a = mean number of alleles, A_r = allelic richness, H_o and H_e = observed and expected heterozygosity, F_{IS} = inbreeding coefficient (* = significant departure from HWE), *Bottleneck*: *P* values of the test for genetic bottlenecks using the TPM mutation model

population	first native record	first non-native record	origin (mtDNA lineage)		*Hapl.*	*N*	n_a	A_r	H_o	H_e	F_{IS}	*Bottleneck*
Mixed populations:												
FRD	Dürigen (1897)	> 1960 (Laufer *et al.* 2007, Fritz pers. comm.)	Southern Alps Tuscany Eastern France	(81%) (17%) (2%)	SA3/6 TU1 EF3	52	8.00	5.40	0.709	0.740	0.051	0.12
FRM	Dürigen (1897)	< 2010 (this study)	Tuscany Eastern France Southern Alps	(59%) (36%) (5%)	TU1/2 EF3 SA6	22	7.00	5.59	0.689	0.733	0.084	0.23
INZ	Dürigen (1897)	< 1998 (Deichsel pers. comm.)	Romagna Venetian Southern Alps	(72%) (21%) (7%)	RO2 VE1 SA5/6	14	6.62	5.82	0.708	0.718	0.052	0.27
LÖR	Dürigen (1897)	> 1998 (Schulte *et al.* 2011a)	Southern Alps Romagna	(78%) (22%)	SA2 RO1/2/3	9	6.31	6.00	0.761	0.727	0.013	0.75
WÖL	Dürigen (1897)	> 1998 (Schulte *et al.* 2011a)	Eastern France Southern Alps	(95%) (5%)	EF2/3 SA2	62	10.46	6.16	0.657	0.735	0.114*	0.88
MAN	Dürigen (1897)	< 2006 (Schulte 2008)	Venetian Southern Alps	(86%) (14%)	VE1 SA4	49	8.39	5.55	0.626	0.697	0.113*	0.71
Purebred introduced populations:												
BRA	-	1982	Southern Alps		SA1	60	6.92	4.18	0.533	0.577	0.085*	0.83
NÖR	-	> 1980	Western France		WF1/2	40	9.08	6.15	0.641	0.678	0.067	0.14
DRE	-	< 1900	Venetian		VE1	63	5.23	3.69	0.562	0.607	0.082	0.19
SCH	-	1964 (10 founders)	Eastern France		EF3/4	64	6.15	3.95	0.572	0.596	0.047	0.42
AMM	-	> 1980	Central Balkans		CB1/2	81	7.92	4.37	0.499	0.587	0.157*	0.66
Purebred native population:												
WIT	Dürigen (1897)	-	Eastern France		EF1	50	5.46	4.00	0.541	0.584	0.083	0.04*

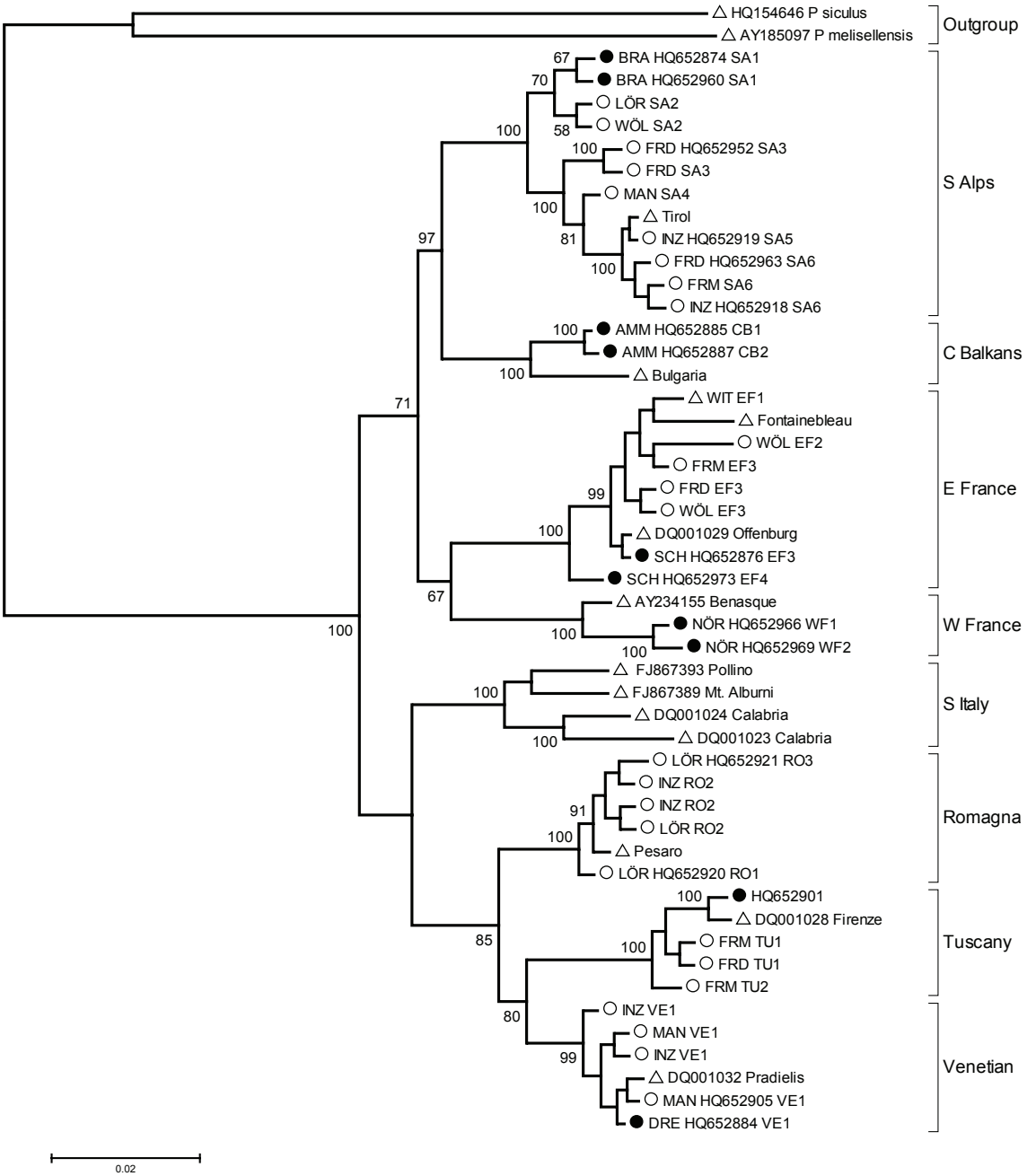

Fig 2: Bayesian consensus tree for the mitochondrial cyt*b* gene for *Podarcis muralis*. Numbers are posterior probabilities. Filled circles represent samples from pure-bred introduced populations, open circles represent samples from mixed populations, open triangles represent samples from native wall lizard populations. Mixed populations = FRD, FRM, INZ, LÖR, WÖL, MAN; purebred introduced populations = BRA, NÖR, DRE, SCH, AMM; purebred native population = WIT. Haplotype abbreviations are given in Table 1.

In locus B4 allele sizes > 135 were only found in populations with founders belonging to the Southern Alps clade. For locus C9, allele sizes > 190 were only found in the NÖR population (Western France origin).

The most likely number of genetic clusters (*K*) among all analysed populations revealed by model-based clustering in STRUCTURE applying the method of Evanno *et al.* (2005) was twelve (Fig. 3). In contrast to our initial sampling, the LÖR population was geographically separated into three

clusters: LÖR, WÖL and INZ. A stepwise increase of K revealed the differentiation of nuclear DNA variation among populations and enabled us to identify lineage-specific genotypes regardless of the haplotype frequencies (see Appendix S2 for K = 1 - 14). At K > 12 intra-population genetic structure occurred, probably caused by hybridization (Fig. 3). From K = 1 - 11 the native population (WIT) always clustered together with the mixed population WÖL, which was predominantly composed of native mtDNA haplotypes (95%). At the maximum ΔK (K = 12) a nearly complete separation of all populations was found.

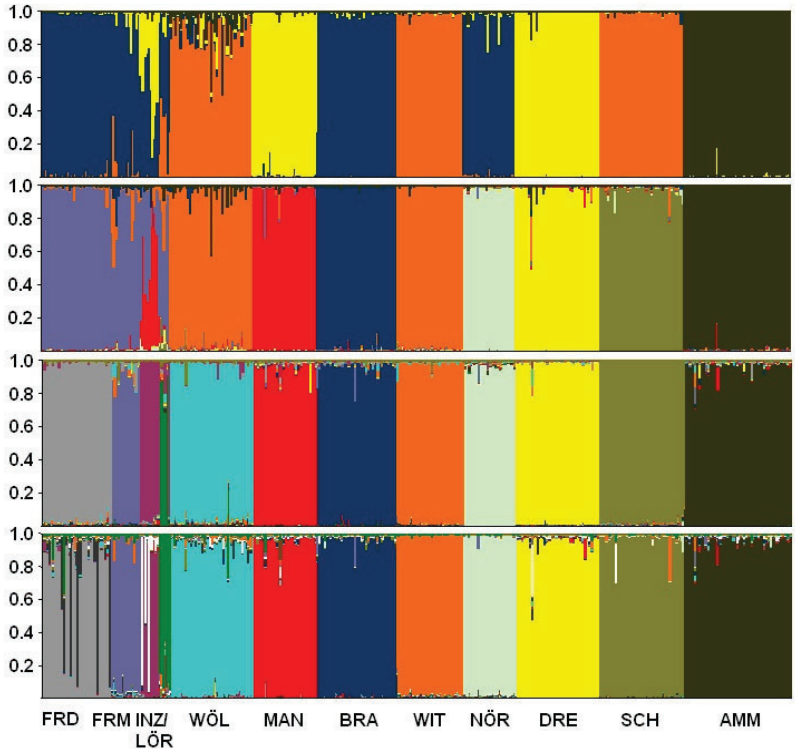

Fig 3: Genetic clusters obtained from the STRUCTURE analysis for all 566 samples (K = 4, 8, 12 and 14). The optimal K according to ΔK was found at K = 12. Each individual is represented by a single vertical line, divided into K colours. The coloured segment shows the individual's estimated proportion of membership to the genetic cluster. Mixed popula-tions = FRD, FRM, INZ, LÖR, WÖL, MAN; purebred introduced popula-tions = BRA, NÖR, DRE, SCH, AMM; purebred native population = WIT.

The strong differentiation among all populations was confirmed by the AMOVA, which revealed that a significant portion (P < 0.001) of the genetic variation occurred among populations (24 % for F_{ST} based, 28% for R_{ST} based AMOVA). Levels of differentiation between all populations were high and significant, with F_{ST} ranging from 0.113 to 0.364 (Table 2), R_{ST} ranging from 0 to 0.588 and D_{EST} ranging from 0.366 to 0.819 (Table 3). For all three measures the lowest differentiation between the native Wittlich and a non-native population was found for the mixed WÖL population (F_{ST} = 0.163, R_{ST} = 0.03, D_{EST} = 0.551) and the SCH population (F_{ST} = 0.168, R_{ST} = 0.011, D_{EST} = 0.399). All these populations were dominated by Eastern France haplotypes (Table 1). The highest differentiation based upon an infinite alleles model was found between the native WIT and the introduced purebred AMM population (F_{ST} = 0.364), which is close to the maximum F_{ST} value possible in this data set (F'_{ST} = 0.88), according to Meirmans & Hedrick (2011). R_{ST} values correlated stronger with the haplotype data, with the lowest values found between populations with similar mtDNA lineage composition (e.g. FRD/FRM: R_{ST} = 0.0).

Table 2: Pairwise F_{ST} values between analysed populations of *Podarcis muralis* (all P values < 0.001).

	FRD	FRM	INZ	LÖR	WÖL	MAN	BRA	WIT	NÖR.	DRE	SCH
FRM	0.123										
INZ	0.143	0.140									
LÖR	0.113	0.122	0.126								
WÖL	0.166	0.159	0.178	0.141							
MAN	0.188	0.156	0.125	0.207	0.218						
BRA	0.209	0.174	0.224	0.238	0.251	0.246					
WIT	0.188	0.236	0.257	0.189	0.163	0.273	0.323				
NÖR.	0.186	0.198	0.183	0.196	0.216	0.208	0.288	0.240			
DRE	0.237	0.240	0.195	0.238	0.241	0.186	0.311	0.330	0.284		
SCH	0.229	0.229	0.251	0.198	0.196	0.268	0.327	0.168	0.190	0.315	
AMM	0.267	0.251	0.252	0.277	0.226	0.251	0.307	0.364	0.297	0.272	0.346

Table 3: Pairwise R_{ST} values (lower left part) and D_{EST} values (upper right part) between analysed populations of *Podarcis muralis*.

	FRD	FRM	INZ	LÖR	WÖL	MAN	BRA	WIT	NÖR.	DRE	SCH	AMM
FRD		0.708	0.682	0.766	0.456	0.510	0.470	0.589	0.664	0.565	0.470	0.625
FRM	0.000		0.783	0.652	0.718	0.569	0.697	0.726	0.508	0.756	0.754	0.772
INZ	0.030	0.000		0.818	0.638	0.719	0.512	0.555	0.796	0.742	0.366	0.524
LÖR	0.117	0.062	0.001		0.707	0.699	0.779	0.589	0.649	0.704	0.819	0.749
WÖL	0.180	0.103	0.097	0.036		0.569	0.524	0.551	0.576	0.475	0.614	0.725
MAN	0.175	0.228	0.270	0.402	0.465		0.524	0.688	0.488	0.586	0.687	0.614
BRA	0.283	0.264	0.198	0.145	0.078	0.588		0.559	0.733	0.672	0.461	0.641
WIT	0.230	0.175	0.155	0.062	0.030	0.528	0.157		0.729	0.642	0.399	0.690
NÖR.	0.279	0.243	0.238	0.226	0.118	0.546	0.394	0.212		0.656	0.751	0.715
DRE	0.130	0.153	0.187	0.280	0.367	0.001	0.442	0.400	0.430		0.710	0.707
SCH	0.227	0.166	0.142	0.049	0.040	0.501	0.114	0.011	0.140	0.404		0.613
AMM	0.226	0.169	0.100	0.038	0.097	0.480	0.073	0.091	0.250	0.390	0.082	

Population specific levels of hybridization

In the mixed populations, we found multiple mtDNA haplotypes, which were mostly not concordant with the genetic clusters obtained from the STRUCTURE analysis. We found different mtDNA lineages within clearly separated STRUCTURE clusters as well as identical mtDNA haplotypes across different clusters, suggesting that large parts of the mixed populations represent completely admixed hybrid swarms.

The population FRD was composed of three genetic clusters (Fig. 1). The most common cluster was found in 77% (N = 40) of the individuals with high Q values (> 0.8), while only four individuals (8%) were assigned to the second cluster (with Q > 0.8) and only low fractions of a third cluster appeared (maximum Q = 0.36). Using a threshold Q-value of 0.2, four individuals of the population were assigned as hybrids between these three clusters (8%). Only one hybrid individual carried the native Eastern France mtDNA haplotype, whereas the other hybrids had Southern Alps clade haplotypes. Within the nearby population FRM 86.4% of the individuals (N = 19) belonged to one cluster (Q > 0.8). Two of the

three individuals with Q values below 0.8 showed admixed genotypes with low fractions of the native cluster found in the population WIT (Q = 0.12-0.13). These two individuals carried also native Eastern France mtDNA haplotypes. In the populations INZ, LÖR and WÖL a total of four genetic clusters occurred. Four individuals were assigned as hybrids between these clusters (4.7%). All other populations were composed of separate genetic clusters, with only three individuals assigned as potential hybrids (0.73 %).

Genetic diversity among populations

Purebred introduced and native *P. muralis* populations had a significant lower genetic diversity (expected heterozygosity H_E) than mixed populations originating from two or more lineages (ANOVA, $F_{2,9}$ = 24.4, $P < 0.001$, Fig. 4). The increase in H_E was not linear and an admixture of a third lineage had nearly no effect on the genetic diversity. The optimal function to describe this correlation was a geometric modified model, with $H_E = 0.605 \times n^{(0.509/n)}$, where n is the number of lineages (r^2 = 0.84). Allelic richness (A_R), H_O and H_E were lower in the native population and purebred introduced populations with low founder numbers than in mixed populations that consisted of two or three lineages (Tab. 1). However, the purebred introduced population NÖR, which retained a high genetic diversity, represents an exception. The lowest values for H_E and H_O were found in the purebred introduced populations AMM and BRA as well as in the native population WIT, which is located at the northern range margin in Rhineland-Palatinate. The inbreeding coefficient (F_{IS}) significantly departs from HWE within the mixed populations WÖL (F_{IS} = 0.114) and MAN (F_{IS} = 0.113) as well as within the purebred introduced populations BRA (F_{IS} = 0.085) and AMM (F_{IS} = 0.157). The lowest inbreeding coefficient was found in the mixed population LÖR (F_{IS} = 0.013) and the purebred introduced population SCH (F_{IS} = 0.047; Tab. 1). Applying the two phase model (TPM) we found evidence for a genetic bottleneck in the native population (P = 0.04, Tab. 1) but not in the mixed or within the purebred introduced populations.

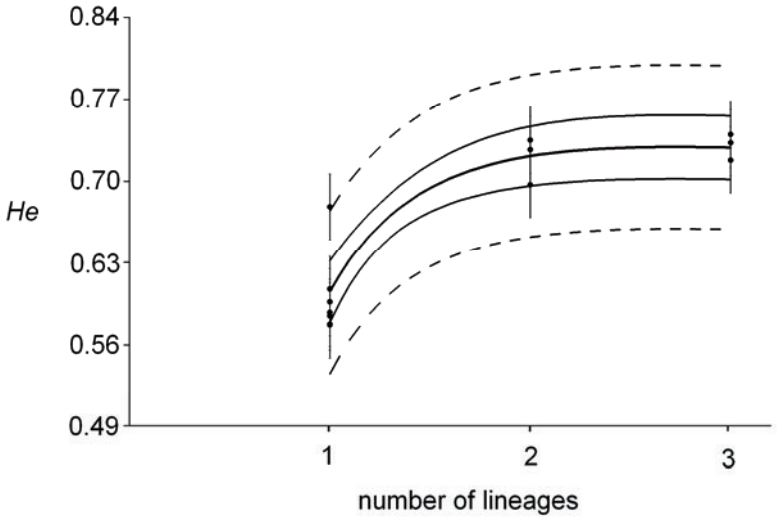

Fig. 4: Correlation between genetic diversity (expected heterozygosity H_E) and number of source lineages. The optimal function to describe the correlation is defined by $H_E = (0.605 \times n \text{ lineages})^{(0.509/n \text{ lineages})}$ (r^2 = 0.84). Upper and lower solid lines show 95% confidence bands, upper and lower dashed lines show predict bands.

Discussion

Our results revealed extensive intraspecific hybridization between introduced wall lizard lineages from Italy and native *P. muralis* populations at the northern range margin. In some mixed populations, the mtDNA signal of the native lineage completely disappeared. In FRD, INZ, LÖR and MAN we found no or only few specimens with native mtDNA haplotypes, while in FRM and WÖL the native haplotypes were still common, but only one fully admixed genetic cluster (based on microsatellites) was found. The extent of introgression and the dominance of Italian haplotypes in mixed populations indicate that most mixed populations have rapidly reached late stages (nearly complete admixture) of a hybrid swarm (according to Brumfield 2010). Our results confirm the hypothesis that the degree of admixture and the source region influence the genetic diversity of introduced populations (Kolbe *et al.* 2004). Altogether, it is reasonable to state that these introductions represent a serious threat to the genetic integrity of native lineages due to the creation of hybrid swarms.

Genetic population structure

Our results confirm a strong genetic differentiation among all populations, regardless of their origin (mtDNA lineage). Even between the mixed population FRD and the nearby mixed population FRM (distance ca. 5 km), which consisted of the same mtDNA lineages, a strong genetic differentiation was found. This is probably caused by the different frequencies of the lineages in these populations (Table 1). Due to the strong genetic structuring, we even had to split the mixed Inzlingen-Lörrach population into three geographically separated subpopulations (INZ/LÖR/WÖL). The strong genetic differentiation at the population level also hampered the use of the purebred native population (WIT) as a reference for detecting native genotypes in most of the mixed populations. Nevertheless, the mixed population WÖL (consisting to 95% of native haplotypes) clustered together with the native population until $K = 11$ and some individuals of the mixed populations also showed low fractions of the "native cluster". Although the inclusion of reference samples is not needed in order to detect hybrids (Vähä & Primmer 2006), such reference samples help to assign hybrids to the correct lineage.

The reasons for the high genetic structure among wall lizard populations remain unknown. In the case of introduced lineages, the different colonization histories, origins and admixture levels of the populations are probably major causes for increasing genetic differentiation (Kolbe *et al*. 2008). It is also likely that introduced populations are strongly influenced by genetic drift (including founder events) during establishment as well as during recent range expansion. Indeed, strong genetic structuring has also been found in invasive populations of the gecko *Hemidactylus mabouia* in Florida at very small spatial and temporal scales (Short & Petren 2011) as well as in other wall lizard populations (Cincinnati, Passau) stemming from a single founder event (Lescano & Petren unpublished data; Schulte unpublished data). Similar patterns can also be found during natural range expansion processes (Hochkirch & Damerau 2009). Therefore, it is possible that rapid genetic structuring due to founder events is a principle pattern of leading edge range extension processes (Hampe & Petit 2005). An additional factor influencing the high

genetic structure in wall lizard populations might be found in the species' pronounced territoriality (Boag 1973, Edsman 1990).

Genetic diversity within populations

Compared to the purebred native and purebred introduced populations the mixed populations exhibited the highest genetic diversity. This positive relationship between genetic diversity and the number of source populations (in our case lineages) in the process of admixture coincides with the pattern found in *Anolis sagrei* in Florida (Kolbe *et al*. 2008). However, our curve fitting approach detected a plateau of high genetic diversity, which was already reached at an admixture level of two. Indeed, a linear relationship between H_E and the number of lineages is unrealistic as by definition $H_E \leq 1$. The high genetic diversity is probably caused by multiple introductions of founders belonging to four different mtDNA lineages originating from the Apennine Peninsula that interbreed with native populations. In contrast, the analysed purebred native population stems from the north-western range margin. A reduced genetic diversity at the edge of range expansions is rather typical due to smaller population sizes, partial isolation, stronger founder effects, genetic drift and higher selection pressure (Böhme *et al*. 2007, Hampe & Petit 2005). Compared to native *P. muralis* populations near Basel, Switzerland (Altherr 2007), genetic diversity in the nearby hybrid populations (INZ, LÖR, WÖL) was rather high and might enhance the species invasiveness (Drake 2006, Ellstrand & Schierenbeck 2000). Since the introduced founders stem from Italy, where multiple Pleistocene glacial refugia and a hotspot of genetic diversity for this species are found (Giovannotti *et al*. 2010, Bellati *et al*. 2011), these individuals might have further increased the genetic diversity by interbreeding with native populations. Levels of inbreeding were quite low except for the mixed populations WÖL and MAN and for the purebred introduced populations AMM and BRA, the latter of which is known to stem from only 16 founders (Tab. 1). Nevertheless, we only found a signal for a genetic bottleneck in the purebred native population WIT, but not in any of the purebred introduced populations. It is possible that the bottleneck of population WIT is a consequence of a founder event or stronger population fluctuations at the northern range margin.

In contrast to the mixed populations, four of the five purebred introduced populations had a rather low genetic diversity. However, compared to a purebred introduced population of *P. muralis* in Cincinnati, Ohio, the genetic diversity was higher in the German introduced populations (Lescano & Petren unpublished data). This was true even for BRA, which has a nearly identical invasion history as the Cincinnati population concerning propagule pressure and origin. This might either be explained by the slightly higher number of founders in BRA ($N = 16$) compared with Cincinnati ($N = 12$), or by a strongly unbalanced reproductive success of the founders in Cincinnati. However, despite the low genetic diversity and multiple bottlenecks in the Cincinnati population, *P. muralis* appears to be a successful colonizer even in North America (Lescano & Petren unpublished data). Inbreeding and a reduced genetic diversity do therefore not necessarily hamper the successful establishment and spread of introduced species

(Ficetola *et al*. 2008, Schmid-Hempel *et al*. 2007).

The presence of different non-native haplotypes from the same lineages in the mixed populations FRD, FRM, INZ and LÖR (Tuscany, Romagna, Southern Alps; Tab. 1) suggests multiple independent introductions of individuals from Italy. In contrast, the populations INZ, DRE and MAN shared identical haplotypes of the Venetian clade (found in the Bologna-Modena region) with 13 non-native populations in Germany (Schulte *et al*. 2011a). We hypothesize that this may be caused by human-mediated secondary introductions, as the independent introduction of founders from the identical restricted source region in 15 cases seems rather unlikely. On the other hand, multiple introductions from different source populations have been found in 35% of the introduced wall lizard populations in which more than two individuals had been sampled (Schulte *et al*. 2011a).

Discordant patterns of mtDNA and microsatellite variation

Our results confirm several recent studies on squamate reptiles in which the combination of nuclear and mtDNA markers revealed discordant patterns (Renoult *et al*. 2009, Zarza *et al*. 2011). One potential reason for this phenomenon is introgressive hybridization linked to sex-biased dispersal. In wall lizards juvenile males are considered the major group of dispersers due to a greater pronounced territoriality of males (compared to females) towards their own sex (Barboult & Mou 1988, Schulte 2008). In fact, discordance of mtDNA variation and (nuclear coded) morphology has also been found at the boundaries of the natural ranges of the Tuscany clade of *P. muralis* and its neighbouring clades, suggesting male-biased gene flow (Mayer, pers. comm. 2011). A second reason for cytonuclear discordance in genetic structure may be found in the different effective population sizes of mitochondria, which are only transferred by the females and only available in one copy. Hence, in diploid organisms mitochondrial N_E is only one fourth of the nuclear N_E (Hedrick 2009). In mixed populations, native mtDNA structure might thus erode four times faster than nDNA.

In our case of anthropogenic intraspecific hybridization two other hypotheses may also explain the incongruence of mtDNA and nDNA variation: (a) directed sexual selection for males stemming from Italy south of the Po river (Venetian clade, Tuscany clade, Romagna clade), or (b) asymmetric interbreeding success (Wirtz 1999). Although the reasons remain unknown, the first hypothesis would fit well with the pattern observed at the native range boundaries of the Tuscany clade. Males belonging to the Venetian, Tuscany and Romagna clades are larger in size and more colourful (Boag 1973, Schulte 2008). Thus, they might have an advantage in territoriality and mate acquisition. The ventral colour of wall lizards correlates with the immune response and is an honest signal of fitness and important during mate choice (Calsbeek *et al.* 2010, López & Martín 2005, Sacchi *et al*. 2007).

Hybridization and its implications for conservation

Problems in distinguishing introduced species or subspecies morphologically from native ones may facilitate introgressive hybridization. As a result the invader remains cryptic until it is abundant, and its eradication becomes almost impossible. This scenario is plausible for *P. muralis*, a species that exhibits a high phenotypic variability in colour pattern at both the intra-specific and intra-population level (Caalsbeck *et al*. 2010, Bellati *et al*. 2011). The only lineages that are relatively easy to distinguish from native wall lizards in Germany by means of their dorsal coloration are the lineages from Central Italy that display partial green dorsal colorations (Schulte *et al*. 2011a). In fact, even for local field-herpetologists it came as a surprise that so many alien haplotypes were found in the mixed population FRM, which we initially had sampled as a purebred native reference population.

Hybridization between introduced and native lineages of species is known to be a serious threat for the genetic integrity and persistence of native species (Dowling & Childs 1992, Rhymer & Simberloff 1996). Local adaptations may get lost through intraspecific hybridization (Allendorf *et al*. 2001) and result in outbreeding depression (Huff *et al*. 2011). This is particularly important for populations at the range border, since they may have developed even stronger local adaptations in order to cope with episodes of unfavourable environmental conditions (e.g. wet and cold early summers in *P. muralis*, Strijbosch *et al.* 1980). It is obvious that a removal of hybrids from mixed populations is impossible. Therefore, conservation activities should primarily focus on the prevention of further human mediated introductions. As the Common Wall Lizard is listed on appendix IV of the EU habitats directive, it is strongly affected by conservation actions. However, as the budget for nature conservation is limited, money should not be wasted in conservation of introduced or mixed populations, even though they belong to the same species and as such should profit from legislation. In cases where compensatory wall lizard translocations are mandatory (as happened in the mixed populations MAN and FRM), genetic analyses will help to avoid the further spread of alien lineages. Rather it is necessary to focus conservation action on maintaining and expanding the remaining native not hybridized populations in urban environments.

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Supplementary material

Appendix S1: Minimum spanning network for the cytochrome *b* haplotypes found in sampled wall lizard populations.

Appendix S2: Development of genetic clusters obtained from the STRUCTURE analysis for all 566 samples for $K = 2$ to $K = 14$.

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Biosketches:

This study is part of the PhD thesis of **Ulrich Schulte**, who is interested in evolutionary consequences of biological invasions and conservation biology with a focus on reptiles and amphibians in Central Europe. **Michael Veith** is interested in the phylogeography, phylogeny and conservation of European fauna, with special emphasize on amphibians and bats of the Mediterranean region. **Axel Hochkirch** is interested in biodiversity research, including evolutionary biology, phylogenetics, ecology, population genetics and conservation biology. He is particularly interested in the ecological significance of species interactions and their importance for nature conservation.

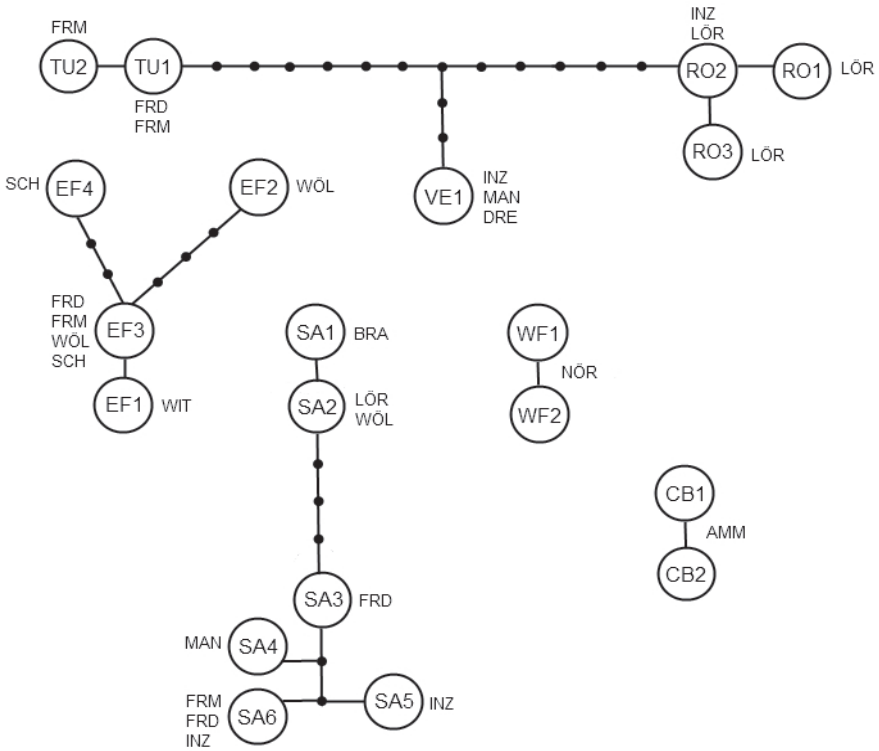
Data Accessibility:

DNA sequences: NCBI Genbank accession numbers JX065611-JX065629;

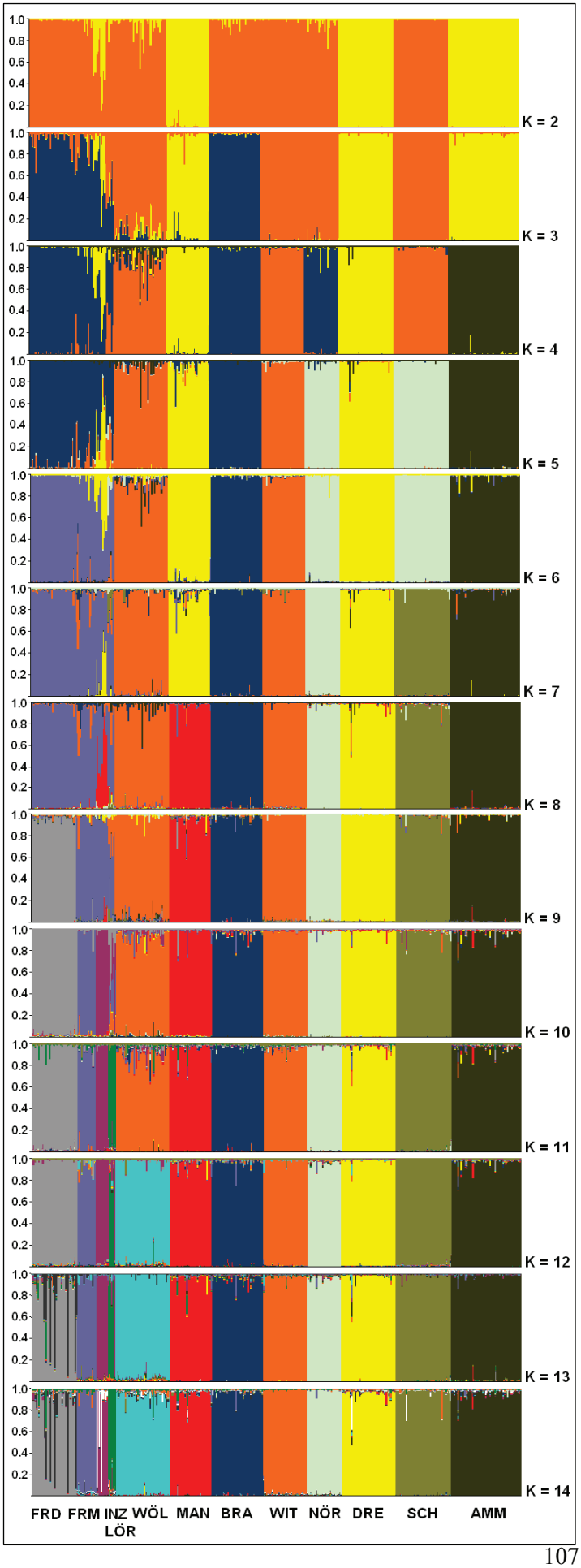
Table, with information about populations, individual ID's, haplotypes and GenBank accession numbers: doi:10.5061/dryad.73c0h

Microsatellite data file and readme.txt file: doi:10.5061/dryad.t5952

Appendix S1: Minimum spanning network for the cytochrome *b* haplotypes found in sampled wall lizard populations. Each circle represents one distinct haplotype (abbreviation inside the circle).
Abbreviations outside the circles illustrate the occurrence of haplotypes in the sampled populations.



Appendix S2: Genetic clusters obtained from the STRUCTURE analysis for all 566 samples for $K = 2$ to $K = 14$. The optimal K according to ΔK was found at $K = 11$. Each individual is represented by a single vertical line, divided into K colours. The coloured segment shows the individual's estimated proportion of membership to the genetic cluster. Mixed populations = FRD, FRM, INZ, LÖR, WÖL, MAN; purebred introduced populations = BRA, NÖR, DRE, SCH, AMM; purebred native population = WIT.



CHAPTER VI

Genetic consequences of a recent range expansion in an introduced wall lizard population

Schulte, U., Hochkirch, A., Mingo, V., Modica, C. & M. Veith: Genetic consequences of a recent range expansion in an introduced wall lizard population. –
unpublished manuscript

Abstract: Fine scale genetic analyses of evolutionary processes acting at the invasion front of expanding populations have been poorly studied. It has been hypothesized that the genetic diversity of invasive populations is decreasing from the centre of the invasion towards the range margins due to multiple founder events. The same mechanisms are thought to increase the genetic structure at the invasion front. We analysed the fine scale genetic structure of a continuous and expanding introduced population of the Common Wall Lizard (*Podarcis muralis*) in Passau, Germany using thirteen microsatellite loci. To reconstruct the history of the range expansion (i) we analyzed the genetic structure and levels of admixture across a transect reflecting the direction of expansion and (ii) we tested for a loss of genetic diversity and an increase of genetic differentiation from the centre of invasion towards the expanding range margin. Available benchmark data of first detections of wall lizards allowed us to estimate the speed of expansion within this invasion event. Our results demonstrate that significant genetic population structure can emerge rapidly at a small spatial scale. The results also showed a trend for an increase in genetic differentiation and decline in genetic diversity from the centre of introduction towards the expanding range margin. Nevertheless, all sites retained rather high levels of genetic diversity. We assume that the pronounced territoriality of *P. muralis* generates sufficient rates of noncontiguous and stratified dispersal from longer established sites to maintain genetic diversity at the invasion front. Simultaneously the territoriality might restrict the acceptance of migrants at established sites, so that a strong differentiation arises. Moreover, we hypothesize that the high spatial population structure could be affected by strong founder events, kin-based dispersal and varying predator abundances across the range. The spread of this population suggest a dynamic range expansion of around 500 meters per year of introduced *P. muralis*. The effective population size was extraordinary high in Passau, exciding most native populations.

Key words: bottleneck, dispersal, founder event, genetic differentiation, invasive species, microsatellite, range expansion;

Introduction

The increase in the rate and spatial extent of alien species introductions is one of the major problems in nature conservation. Therefore, a considerable amount of research has been carried out to identify the mechanisms that drive biological invasions and to evaluate their impact on native ecosystems in order to develop mitigation strategies for the future (Strayer *et al*. 2006, Perrings *et al*. 2010). While most studies have pronounced factors that facilitate or hamper invasion processes at large spatial and temporal scales (e.g. Elton 1958, Sakai *et al*. 2001, Colautti *et al*. 2004, Pyšek & Richardson 2007, Simberloff 2009), there is a considerable lack of fine scale genetic studies on the consequences of range expansions for the invasive population itself, which could offer important insight into the intrinsic factors that determine invasion success (Ramakrishnan *et al*. 2010). Moreover, questions addressed in such studies are rather similar to important questions when examining natural range expansions, habitat shifts and adaptive evolution under climate change scenarios (Thomas *et al*. 2001). Most genetic studies either focus on the divergence of invasive populations from their ancestral source population (Bossdorf *et al*. 2005, Lockwood *et al*. 2007) or investigate genetic structure at larger geographic scales (Eckert *et al*. 2008). Only a few studies address the interplay between genetic variation and range expansion at small spatial and temporal scales in founding populations (Herborg *et al*. 2007, Dlugosch & Parker 2008, Parisod & Bonvin 2008, Björklund & Aronson 2010, Short & Petren 2011).

In theory it is expected that within-population genetic diversity is declining towards the range margins of a species, whereas the genetic differentiation among populations increases (Brussard 1984, Thomas *et al*. 2001, Eckert *et al*. 2008). Genetic diversity is thought to decrease due to recurrent founder effects, small effective population sizes, partial isolation, stronger genetic drift and higher selection pressure (Hewitt 2001, Böhme *et al*. 2007). Virtually all introduced species experience changes in allele frequencies due to genetic drift (mainly caused by founder events). These effects leading to sharp allele frequency gradients might be the key drivers for genetic differentiation in nascent colonizing populations at the expansion front (Excoffier & Ray 2008). Moreover, it has been shown that negative effects of founder events, such as a loss of genetic diversity, are not necessarily hampering the spread and adaptive evolution (life history variation) within nascent populations (Dlugosch & Parker 2008). Indeed, recent studies have documented a recombination among source genotypes (Dlugosch & Hays 2008), a surfing of low-frequency alleles at the wave front of expansion (Excoffier & Ray 2008) and a purging of alleles that cause inbreeding depressions (Facon *et al*. 2011). It has been assumed that these mechanisms are particularly important during spatial expansions of invasive species (Facon *et al*. 2011). Furthermore, it is thought that negative effects of founder events can be diminished to some extent by gene flow through stratified dispersal and reshuffling effects during range expansions (Eckert *et al*. 2008, Parisod & Bonvin 2008).

The distribution of genetic variability over space and time in expanding populations is strongly associated with the dispersal mode of an introduced species (Estoup *et al*. 2004, Wilson *et al*. 2009). However, there is very little information available on dispersal modes and their contribution towards

fluctuations in effective population sizes at the edge of rapid range expansions (Estoup *et al*. 2004, Ramakrishnan *et al*. 2010). Across all geographic scales frequent contiguous (diffusion) and less-frequent non-contiguous (long-distance) dispersal is expected and has been assumed in various models of migration: island model of migration (Wright 1942), stepping-stone model (Kimura & Weiss 1964), and isolation by distance (Wright 1942). Diffusion is leading to a gradual spread over a period of generations (classic isolation by distance pattern), while long-distance dispersal is thought to result in the establishment of pioneer clusters far away from the source, often exhibiting severe genetic bottlenecks (Petit *et al*. 1997, Wilson *et al*. 2009). Interestingly, a recent study on the invasive grass *Brachypodium sylvaticum* in Oregon indicates that dispersal modes can change along the time scale of invasions (Ramakrishnan *et al*. 2010). Early colonization processes at the invasion front are mainly driven by long-distance dispersal, whereas during the subsequent stages of establishment diffusion becomes more important for immigration (so called "stratified dispersal" Shigesada *et al*. 1995). In addition to behavioural and life history traits as well as landscape patterns which are known to shape the dispersal mode and rate, human assisted jump-dispersal (particularly in urban areas) and the admixture of different founder individuals might also act as major contributors for the genetic structure of expanding populations (Kolbe *et al*. 2008, Wilson *et al*. 2009, Chapple *et al*. 2012).

Recent fine scale genetic analyses of range expansions provided evidence that significant genetic structure can arise at very small spatial and temporal scales (Short & Petren 2011). Thriving invasive populations provide ideal conditions to study spatial and temporal patterns of genetic variation during colonization events. In this study, we assess spatial patterns of genetic structure and genetic diversity within an introduced and expanding population of the Common Wall Lizard (*Podarcis muralis*) in south-eastern Germany. *Podarcis muralis* is a synanthropic lacertid lizard with a sub-Mediterranean native distribution, which has successfully colonized regions in Central Europe and North America far outside its native range. Up to now more than 160 self-sustaining populations are known (Schulte 2008). We here focus on the largest known invasive population of this species, which is found in Passau, Germany. For this population the geographic origin and parts of the invasion history have been documented (Schulte *et al*. 2011b, 2012a). The population stems from founder individuals from the Bologna-Modena area (Venetian Clade), which have been presumably introduced in the 1930ties or 1940ties (Lentner 1936, personal comm. of residents). The species has currently colonized a range of about 25 kilometres and crossed the Austrian border (Schulte 2008).

In order to study the genetic consequences of the invasion history, we used nuclear microsatellite markers i) to examine the genetic structure across a transect covering nearly the entire continuously colonized range and reflecting the colonization history, and ii) to test the hypothesis for a loss of genetic diversity and an increase of genetic differentiation at the expanding range margin.

Materials and methods

Sampling

In August 2009, a total of 155 lizards (juveniles and adults of both sexes) were captured by hand or by noosing in Passau (Fig. 1). To cover the routes of expansion across the complete colonized range, we randomly sampled individuals at five sites along a 18 km long transect from Hals to Obernzell (HA: N = 19; VE: N = 42; PA: N = 34; ER: N = 29 and OB N = 31; Fig. 1). Since only the initial introduction site (VE) and the direction of expansion (from West to North (HA) and to East (OB)) was known, residents were asked about times of first sightings of wall lizards in order to obtain benchmark data that document their spread since introduction. It is thought that the species has colonized HA in the 1960ties and PA after establishment at site VE in the 1930ties or 1940ties. Site OB has to be considered as the most recently colonized one (before 1975, Assmann 1977, Froer 1980) close to the edge of the expansion at neighboring sites at the Austrian border. Since the mid 1970ties the abandoned Danube railway track from Passau to Obernzell has been colonized (Assmann 1977), afterwards the species has spread into urban areas and lateral valleys.

DNA samples were collected by buccal swabbing each specimen using a diagnostic fine-tip dry swab (Medical Wire & Equipment, MW-100) (Schulte *et al*. 2011a). Samples were stored in sterile tubes at -20°C until DNA was extracted using the Qiagen DNEasy blood and tissue kit following the manufacturer's protocol (adding PBS buffer).

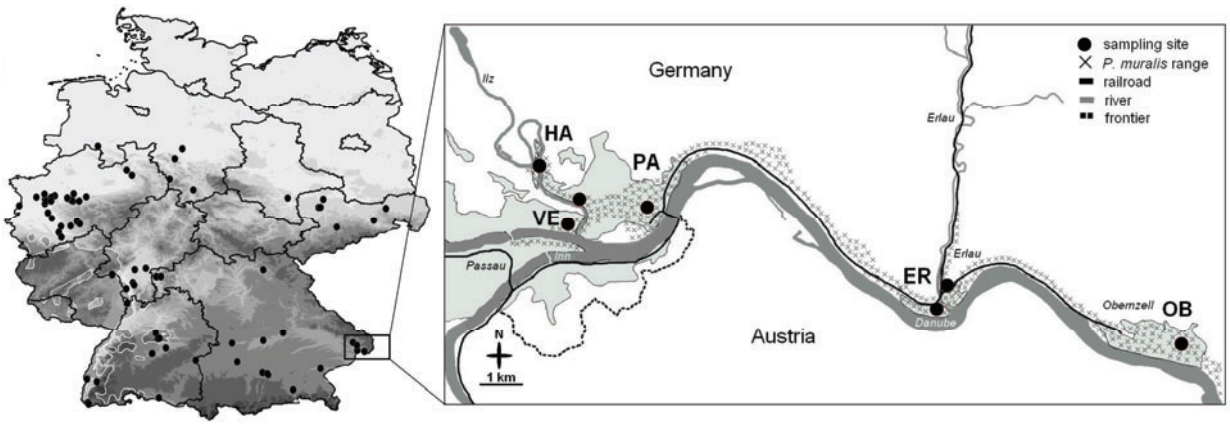


Fig. 1: Native (grey area in the Southwest delimited by a white line) and invasive (black dots) distribution of *P. muralis* (Schulte 2008) and location of the study site in Germany as well as location of sampling sites across the colonized range of the species in the Passau region in Germany (Abbreviations: HA, Hals (Ruine), VE, Veste Oberhaus, PA, Passau-Grubweg, ER, Erlau, OB, Obernzell). VE was the initial introduction site, from where the colonization took place from West (older sites) to North and East (newer sites).

Genotyping

We genotyped 155 individuals of the population at thirteen microsatellite loci, which have been developed for *Podarcis muralis* (A7, B3, B4, B6, B7, C8, C9; Nembrini & Oppliger 2003), *Zootoca vivipara* (Lv-319, Lv-4-alpha, Lv-472; Boudjemadi *et al*. 1999) and *Podarcis bocagei* (Pb10, Pb50, Pb73; Pinho *et al.* 2004). Amplification was performed in a Multigene Gradient Thermal Cycler (Labnet) using

the Qiagen Multiplex Mastermix or 5PRIME HotMasterMix. Multiplex PCRs were run for a combination of two to three loci with variable annealing temperatures (C9/B4/Pb73: 57°C; B3/Pb10/Lv319: 56°C; Lv472/Pb50: 53°C; A7/Lv4alpha: 60°C; A7/B7: 60°C). Multiplex PCRs were performed in 10 µl reaction mix containing: 1.4 µl genomic DNA, 5.5 µl MultiplexMasterMix, 2.9 µl water and 1.1 µl primer-mix. PCR conditions were used as recommended by the manufacturer. For primers C8 and B6 we used singleplex PCRs in a 5 µl reaction mix containing: 1.2 µl genomic DNA, 2.2 µl 5Prime MasterMix, 2.2 µl water and 0.1 µl of the forward and reverse primers at the locus-specific annealing temperature of 57°C. The 5'-end of each forward primer was labelled with a fluorescent dye, either FAM, TAMRA or HEX. PCR products were run on an MEGABACE 1000 automated sequencer. Fragment lengths were determined using Fragment Profiler 1.2 (Amersham Biosciences).

Data analysis and descriptive statistics

We tested our data for the occurrence of null alleles in Micro-Checker 2.2.3 (Van Oosterhout *et al*. 2004) and for linkage disequilibrium in Fstat 2.9.3.2 (Goudet 1995). STRUCTURE 2.3.3 (Pritchard *et al*. 2000) was used to detect genetic structure among sites in the population. The admixture model was used as we expected gene flow among sites. The admixture proportion Q of each individual as an estimate of an individual's proportion of ancestry from each cluster (site) was obtained by STRUCTURE to separate admixed from purebred individuals at sites (Vähä & Primmer 2006). We chose a conservative threshold value of Q = 0.20-0.80 for the detection of admixed individuals, since values outside this range tend to overestimate admixture processes (see also Randi 2008, Sacks *et al*. 2011). We chose the correlated allele frequency model with a burn-in of 50,000 simulations followed by 500,000 Markov chain Monte Carlo simulations. Tests were run for K = 1-6 with 15 iterations per K. To infer the optimal K value from STRUCTURE runs we used the method described by Pritchard *et al*. (2000) as the method suggested by Evanno *et al*. (2005) tends to result in too low values (Wilkinson *et al*. 2011) and our lnPD values showed no asymptotic convergence, but a clear optimum. We used STRUCTURE HARVESTER (Earl & vonHoldt 2011) to analyse the results.

We used GenAlEx 6.4.1 (updated from Peakall & Smouse 2006) to calculate the number of alleles (n_a), the inbreeding coefficient (F_{IS}), as well as expected and observed heterozygosities (H_e and H_o) for each locus and site. FSTAT was used to calculate allelic richness (A_R) among sites (Goudet 2001). Although the use of F_{ST} as a measure of population differentiation has been strongly debated (e.g. Jost 2008, Gerlach *et al*. 2010), it has been shown to be still useful, particularly if Hardy-Weinberg conditions are met (Ryman & Leimar 2009, Meirmans & Hedrick 2011). We calculated F_{ST} in an AMOVA with 9999 iterations in GenAlEx with the genetic clusters suggested by STRUCTURE as populations (Ryman & Leimar 2009). We tested for a correlation between genetic diversity (A_R) and average pairwise F_{ST} and geographic distance among sites with a Spearman rank test in R 2.14.0. Furthermore, we tested for a correlation between A_R and average pairwise F_{ST} without considering the geographic distance among sites with a Spearman rank test in R 2.14.0. To test whether dispersal followed the pattern of isolation by

distance, we calculated the geographic distance using the riverbanks and railway track from Hals to Obernzell. Isolation by distance was tested for significance using a Mantel test with 1000 permutations in the isolation by distance web service (IBDWS) version 3.22 (Jensen *et al*. 2005).

We estimated the effective population size (N_e) for the entire population using ONeSAMP, which uses an approximate Bayesian computation for estimating N_e and 95% confidence limits (CL) (Tallmon *et al*. 2008). The program generates 50.000 simulated populations with N_e between a conservatively estimated lower and upper bound for N_e (2-5000). After executing five iterations of estimating N_e we calculated the mean and standard deviation of N_e for all sites pooled.

In order to detect recent bottlenecks the program BOTTLENECK 1.2.02 was used (Cornuet & Luikart 1996). Recent bottlenecks (0.2 – 4 *Ne* generations) can create a heterozygosity excess compared to populations at mutation-drift equilibrium because rare alleles that have little impact on heterozygosity can be lost quickly. We calculated *Heq* using the two-phase model (TPM, Di Rienzo *et al*. 1994) as this is believed to be the most likely mutation model for microsatellites (Piry *et al*. 1999). Statistical significance was assessed with a one-tailed Wilcoxon-test, which has been recommended for microsatellite data with fewer than 20 loci (Piry *et al*. 1999). Analyses were performed with 1000 iterations.

Results

Population structure and genetic differentiation

All microsatellite markers proved to be polymorphic. We found evidence for null alleles at one to five loci in the five genetic clusters suggested by STRUCTURE (see below). Since no locus showed evidence for null alleles across all sites and nearly all Oosterhout values were below 0.2, all loci were kept for further analyses. There was no evidence for large allele drop-out or other scoring errors and all pairwise tests for linkage disequilibrium were non-significant ($P > 0.05$). The most likely number of genetic clusters (K) within the Passau population revealed by model-based clustering in STRUCTURE was five (Fig. 2).

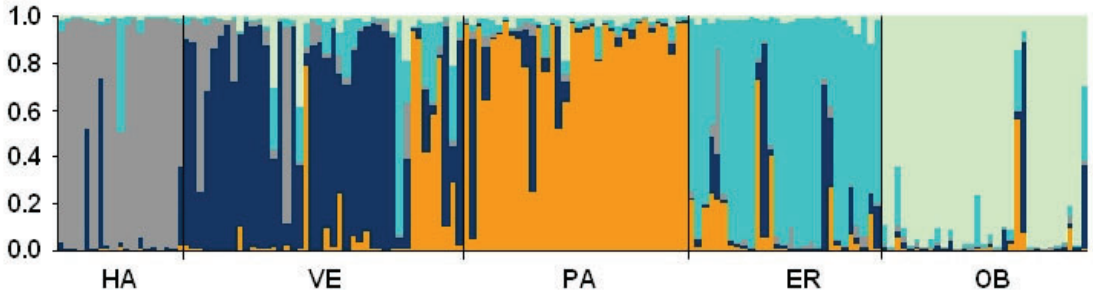


Fig. 2: Genetic clusters obtained from the STRUCTURE analysis (K = 5) for all 155 samples. Each individual is represented by a single vertical line, divided into K colours. The coloured segment shows the individual's estimated proportion of membership to that genetic cluster. HA, Ruine Hals; VE, Veste Oberhaus; PA, Passau Grubweg; ER, Erlautal; OB, Obernzell.

The clear separation into five clusters closely reflects the sampling sites. The AMOVA revealed that a significant part of the genetic variation (7%; $P < 0.001$) exists among sites. We found a strong genetic differentiation between all sites even at a small geographical scale. All pairwise F_{ST} values were significant (Tab. 1). F_{ST} values ranged between 0.038 and 0.138 with the maximum found between HA and OB at the two leading edges of the colonized range. The average F_{ST} value was lowest for VE and highest at the range margin (HA and OB, see Fig. 3b). However, no significant isolation-by-distance was found (Mantel test, $R^2 = 0.0458$, $P = 0.305$, $N = 10$ pair-wise comparisons).

Table 1. Pairwise F_{ST} values (lower left part) among sampling sites. All pairwise F_{ST} values were significant.

	HA	VE	PA	ER	OB
HA					
VE	0.069				
PA	0.129	0.042			
ER	0.074	0.038	0.062		
OB	0.138	0.062	0.079	0.093	

Three of the five sites were composed of genetically rather homogeneous clusters, whereas at two sites several genetic clusters were found (VE and ER; Fig. 2 and 3c). HA was composed of one main genetic cluster (78.9% of the individuals with Q values > 0.8), while 21.1% were assigned as admixed individuals (mostly between HA and the neighboring VE). The nearby site VE shows large proportions (40.5%, see Fig. 3c) of mixed ancestry between four different clusters of the adjacent sites: HA, VE, PA and ER. 54.8% (N = 15) of all individuals were assigned to the cluster VE. The next cluster PA was the most homogeneous cluster with 79.7% (N = 27) of all individuals belonging to one main cluster (PA), and only 8.8% admixed individuals. Admixture was most prominent between clusters PA and VE, but absent between PA and other sites (HA, ER, OB).

ER shows similar large proportions of mixed ancestry (37.9%) like VE, while 55.2% (N = 16) of all individuals belonged to the most common cluster (ER) (Fig. 3c). Gene flow was strongest between ER and VE and PA, but lacking with site OB. The last cluster of OB represents a rather homogeneous cluster (83.9% represent the main cluster OB, N = 26) with only 16.1% admixed individuals. The cluster showed gene flow with all other sites, except with site HA.

Genetic diversity across the range

We found no correlation between genetic diversity and geographic distance among sites. However the correlation between genetic diversity (A_R) and average pairwise F_{ST} was significant ($R^2 = 0.80$, df = 3, t = -3.45, $P = 0.041$). All sites retained a rather high genetic diversity with an allelic richness ranging from 5.17 for OB and 6.30 for VE (Tab. 2). Sites at the range border (HA and OB) had the lowest allelic richness, whereas VE, the centre of introduction, retained the highest allelic richness (6.30, Fig. 3a).

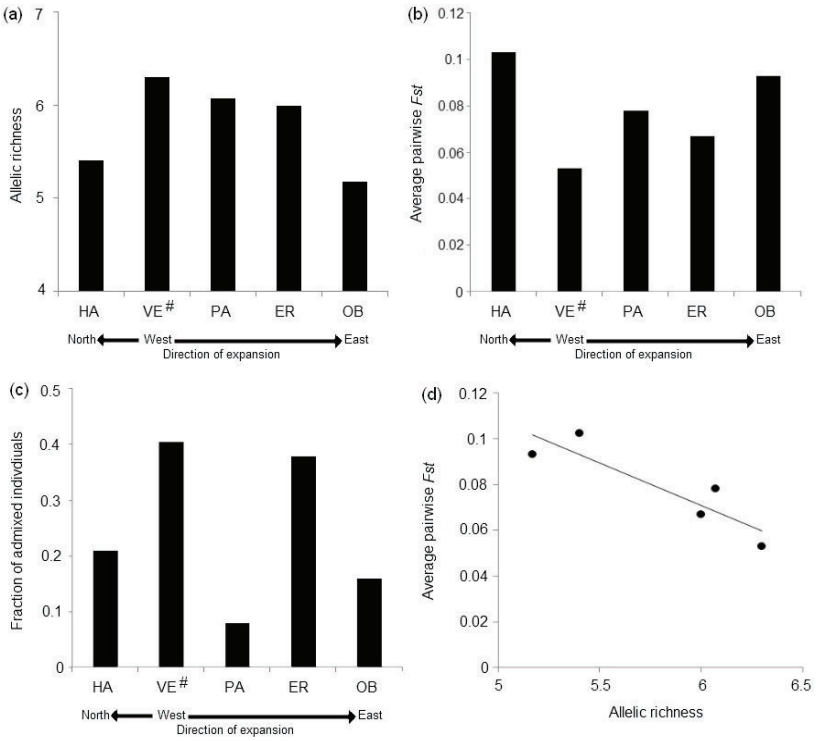


Fig. 3: Relationship between direction of expansion (VE# = presumed introduction site) and (a) allelic richness, (b) genetic differentiation, (c) the fraction of admixed individuals at sites and (d) correlation of genetic diversity and genetic differentiation.

The expected heterozygosity showed a concordant pattern (VE = 0.76; OB = 0.67). Among all sites the inbreeding coefficient (F_{IS}) was not significant. F_{IS} was highest at OB (F_{IS} = 0.15) and rather low at HA (F_{IS} = 0.03). We found evidences for genetic bottlenecks (heterozygote excess) at HA, VE and ER when we applied the two phase model (TPM). The estimated N_e of the entire population (all sites combined) was 840 ± 3.69.

Table 2. Comparison of genetic variability among sites; N = number of samples, N_A = mean number of alleles, A_R = allelic richness (corrected for the minimum sample size of 19 individuals), H_O & H_E = observed and expected heterozygosities, F_{IS} = inbreeding coefficient (* = significant departure from HWE), *Bottleneck*: *P* values of the test for genetic bottlenecks using the TPM mutation model.

Site	*N*	N_A	A_R	H_O	H_E	F_{IS}	*Bottleneck*
HA	19	5.62	5.40	0.69	0.71	0.03	0.03*
VE	42	7.70	6.30	0.67	0.76	0.12	0.0002*
PA	34	7.31	6.07	0.66	0.72	0.08	0.19
ER	29	6.80	6.00	0.69	0.75	0.08	0.0006*
OB	31	6.15	5.17	0.57	0.67	0.15	0.34

Discussion

Our results clearly show that during the invasion process of wall lizards at Passau a small scale genetic population structure rapidly arose. This comes as a surprise when considering the small geographic distance between sites (mean 9.7 km), the high mobility of the species (Schulte 2008) and the existence of suitable dispersal corridors. However, our result supports recent findings from the range expansions of other invasive species (Dlugosch & Parker 2008, Ramakrishnan *et al.* 2010, Short & Petren 2011). The geographic patterns of genetic variation strongly matches the patterns found in natural ranges of species (Eckert *et al*. 2008, Hampe & Petit 2006). Although not significant, we also found a decrease in genetic

diversity from the centre of the invasion towards its front line. In contrast, genetic differentiation was stronger at the range margin, suggesting that genetic drift plays an important role during the range expansion process. Such a significant association between a reduced within-population genetic diversity and increasing among-population differentiation towards the range margin of species has been supported by only a few studies (reviewed in Eckert *et al*. 2008).

Rapid genetic differentiation

The reasons for the strong genetic structure among all populations remain unknown, but it seems unlikely that geographic distance alone explains this pattern. The isolation by distance pattern was not significant, and even closely situated sites (e.g. HA/VE: 1.6 km) were highly differentiated. However, the tendency for stronger genetic differentiation at the range margin suggests that the number of dispersing individuals is small enough to allow for rapid changes due to genetic drift (Björklund & Almqvist 2010). Similar patterns have been found in invasive populations of the gecko *Hemidactylus mabouia* in Florida at very small spatial and temporal scales (Short & Petren 2011) as well as in a North American wall lizard population (Cincinnati) stemming from a single founder event (Lescano 2010).

In addition to founder effects, the invader's behaviour during the invasion process may also affect the resulting genetic population structure (Holway & Suarez 1999). Kin-based colonization with high levels of relatedness at sites producing a large number of good colonizers has been shown for the common lizard *Zootoca vivipara* (Cote *et al*. 2007) and may also be important in *P. muralis* Furthermore, the pronounced territoriality of wall lizards may also foster a pronounced spatial structuring. In *P. muralis* populations resident adult males defending their home ranges and monopolizing females, while floating individuals of different age without home ranges form a stock of dispersers (Boag 1973, Edsman 1990). In addition, territoriality may restrict the acceptance for migrants at established sites, so that population differentiation will further increase. Within isolated and extremely dense introduced populations of the wall lizard (e.g. Ammelshain, Steinicke *et al*. 2000; Cincinnatti, Brown *et al*. 1995) a decrease of home range size was observed. The Passau population may differ from these examples, as it is situated in a suitable area with many unoccupied habitats and suitable dispersal pathways to connect them. It is thus likely that in Passau floating individuals become dispersers rather than competitors for already occupied territories. On the other hand, the continuous dispersal of floating individuals should decrease genetic differentiation in the long run. Indeed, this pattern might explain, why nascent sites (OB, HA) are stronger differentiated than the older ones.

Dispersal pattern

The observed genetic patterns are in line with the stratified dispersal model (Ramakrishnan *et al*. 2010). Founder events and strong genetic differentiation at the range margin suggest that long distance dispersal is the main driver of new colonization events, whereas older populations are stronger connected by

dispersal. Since isolation-by-distance was not significant, we assume that diffusion is not the predominant dispersal pattern.

Based upon the historical records, the mean speed of the range expansion from West to East was around 500m/year. Similar expansion rates per year (440m/year) have been found in an introduced population in Liechtenstein (Kühnis & Schmocker 2008) and in the introduced wall lizard population in Cincinnati (350m/year; Hedeen & Hedeen 1999). Movement distances of *P. muralis* inferred from mark-recapture studies range from 50m/h to 500m/1-3 years (Schulte 2008). However, maximum movement distances of up to 1000m/day have been documented for juveniles, suggesting a stronger dispersal ability of this cohort (Stumpel 2004). Furthermore, it is likely that mark-recapture analyses notoriously underestimate the species' dispersal ability since 40-60 % of the lizards marked in these studies were never recaptured (Boag 1973, Dexel 1984, Brown *et al*. 1995). It is sound to assume that the abandoned Danube railway tracks act as major dispersal corridors. In addition, the species might also have used rocky outcrops, rubbish piles and limestone walls for dispersal. In fact, other introduced *P. muralis* populations have also mainly used railroad tracks, but even high traffic streets did not hamper their spread (Hedeen & Hedeen 1999, Kühnis & Schmocker 2008). However, beside natural dispersal we cannot rule out that human mediated jump-dispersal may have facilitated the rapid range expansion of the population.

Genetic diversity across the range

The total Passau population has a high genetic diversity comparable to that found in mixed populations rather than to other purebred introduced and native wall lizard populations in Central Europe (Altherr 2007, Chapter V) (see Chapter V and values found within an introduced population originating from the Pyrenees; Schulte *et al*. 2012b). This may be due to the source area of the founder individuals, which stem from the northern slopes of the Apennine where Pleistocene glacial refugia of this species have existed and a hotspot of genetic diversity can be assumed (Blondel & Aronson 2010, Giovannotti *et al*. 2010, Belatti *et al*. 2011). It is also likely that propagule pressure during introduction was rather high (high number of founders or introductions). A large propagule size has been documented from a nearby population in Linz, Austria (130 introduced individuals; Schulte 2008) and may be rather a rule than an exception. The estimated effective population size in the Passau population (840 ind.) is very high and exceeds effective population sizes found in other introduced and many native populations in Central Europe. The rapid establishment and extensive spread of the species can most likely be explained with the very suitable habitat, including various dispersal corridors and the missing competition.

There was a trend of decreasing genetic diversity from the presumed initial introduction site towards more recently colonized sites at the leading edge of the population, which is in line with theoretical models of genetic processes during range expansions (Hampe & Petit 2006) and has been also found in other fine scale genetic analyses of range expansions (Short & Petren 2011). The decline of genetic diversity is following the direction of expansion and is most likely the result of time-dependent fluctuations of effective population sizes (population growth after founder events). In contrast, continuous

gene flow among adjacent populations might have generated the higher genetic diversity close to the introduction site at VE.

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Chapter VII

Verbreitung, geografische Herkunft und naturschutzrechtliche Aspekte allochthoner Vorkommen der Mauereidechse (*Podarcis muralis*) in Deutschland

Distribution, geographic origin and legal aspects of introduced wall lizard populations (*Podarcis muralis*) in Germany

Schulte, U., Bidinger, K., Deichsel, G., Hochkirch, A., Thiesmeier, B. & M. Veith (2011): Verbreitung, geografische Herkunft und naturschutzrechtliche Aspekte allochthoner Vorkommen der Mauereidechse (*Podarcis muralis*) in Deutschland. –
Zeitschrift für Feldherpetologie 18: 161–180.

Zusammenfassung: Vor drei Jahren wurde der erste Versuch unternommen, eine möglichst komplette Übersicht über allochthone Mauereidechsen-Vorkommen in Deutschland zu erhalten. Die vorliegende Zusammenstellung ist eine Aktualisierung der Liste mit neuen Ergebnissen. Neben Angaben zur Verbreitung und zum Lebensraum von 82 Populationen, präsentieren wir Informationen zum vermuteten oder recherchierten Ursprung, zum Alter sowie zu geschätzten Bestandsgrößen. Die bereits publizierten Ergebnisse einer bundesweit durchgeführten genetischen Herkunftsanalyse der Populationen werden zusammengefasst, ergänzt um weitere aktuelle Ergebnisse. Darüber hinaus werden Angaben zur Hybridisierung mit heimischen Mauereidechsen sowie zur Sympatrie mit Zauneidechsen (*Lacerta agilis*) gemacht. Entscheidungshilfen zur phänotypischen Unterscheidung invasiver Linien werden präsentiert und die naturschutzrechtlichen Konsequenzen einer innerartlichen Verschleppung diskutiert.

Schlüsselbegriffe: mtDNA, Morphologie, evolutionäre Linien, Unterarten, *Podarcis muralis*, invasive Arten, Naturschutzrecht, Deutschland.

Abstract: Three years ago, a first attempt was undertaken to present an overview on introduced wall lizard populations in Germany. This present compilation is an update of the list with new results. Besides data on the distribution and habitat of 82 populations, we provide information on presumed or known sources, ages, as well as on the estimated population sizes. The results of a genetic analysis of the geographic origin of the German populations have already been published and are summarised here with some additional new results. Furthermore, information on hybridisation with native wall lizards as well as information on the sympatry with sand lizards (*Lacerta agilis*) is presented. An approach for the phenotypic assignment of populations to evolutionary lineages is given and the problem, how to deal with invasive populations is discussed in the light of the current conservation legislation.

Key words: mtDNA, morphology, evolutionary lineages, subspecies, *Podarcis muralis*, invasive species, environmental law, Germany.

Einleitung

Im Rahmen einer Monografie über die Mauereidechse (SCHULTE 2008) ergab eine Befragung von Experten (Feldherpetologen und Naturschützer), dass Mauereidechsen unbekannter Herkunft in Deutschland an 72 Orten eingeschleppt wurden (SCHULTE et al. 2008). Das Ausmaß der aktiven oder passiven Verschleppung einer Eidechsenart in Deutschland war überraschend, und es wurden nachfolgend weitere Untersuchungen eingeleitet. In einem ersten Schritt wurde die Herkunft von insgesamt 77 bekannten Vorkommen aus Deutschland, Österreich, Liechtenstein und der Schweiz in Kooperation mit WERNER MAYER und SILKE SCHWEIGER bestimmt und getestet, inwieweit die klimatische Eignung des Aussetzungsraumes im Vergleich zur Klimanische der jeweiligen Linie im natürlichen Areal den Erfolg der Etablierung beeinflusst (SCHULTE et al. 2011b). Darüber hinaus wurden zahlreiche Populationen in Kontaktzonen, in denen eingeschleppte Individuen auf indigene Bestände treffen, untersucht, um Aufschluss über das Ausmaß der genetischen Vermischung als wichtigen Faktor von Invasivität zu erhalten. Gegenwärtig wird die Ausbreitungshistorie zahlreicher langjährig etablierter Populationen molekulargenetisch rekonstruiert sowie die Konkurrenz mit anderen Lacertiden (v. a. Zauneidechse) überprüft. In der vorliegenden Arbeit werden die Ergebnisse der genetischen Herkunftsanalyse der allochthonen Populationen in Deutschland zusammenfassend präsentiert, ergänzt um weitere aktuelle Ergebnisse. Neben Angaben zur Verbreitung der Populationen, werden Angaben zum Lebensraum, dem Jahr der Entdeckung, dem vermutlichen oder recherchierten Ursprung, der Populationsgröße sowie Bemerkungen zur Hybridisierung mit heimischen Beständen und Interaktionen mit Zauneidechsen gemacht. Darüber hinaus werden der aktuelle rechtliche Status und der naturschutzfachliche Umgang mit allochthonen Mauereidechsen-Vorkommen diskutiert und Handlungsempfehlungen gegeben.

Methoden

Insgesamt wurden 366 Mauereidechsen aus 77 allochthonen Populationen in Deutschland mittels Fangschlinge und Handfang verletzungsfrei gefangen. Ergänzend zur Methode der Gewebebeprobung, bei der die Eidechsen durch leichten Druck am Schwanzende zur Autotomie eines kleinen Stückes veranlasst werden, wurde ein Teil der untersuchten Individuen mittels Mundschleimhautproben untersucht. Dabei kamen sowohl diagnostische Abstrichstäbe (Medical Wire & Equipment, MW-100) als auch handelsübliche zurechtgeschnittene Ohrenstäbchen zum Einsatz. Etwa eine Minute lang wurden Abstriche von Zungenboden, Backen und Gaumen von jedem Individuum genommen. Hierbei zeigte sich, dass Mundschleimhautproben sehr gut zur DNA-Gewinnung bei Lacertiden genutzt werden können. Vorteilhaft bei dieser Art der Beprobung ist neben der Tier schonenden Probengewinnung, die im Gegensatz zu Gewebeproben weder die Kletterfähigkeit noch den Fettvorrat der Eidechsen beeinflusst, die große Zeitersparnis bei der DNA-Extraktion (SCHULTE et al. 2011a). Die geografische Herkunft von allen 366 Mauereidechsen wurde mit Hilfe eines Sequenzvergleichs (Sequenzierung eines 650bp langem

Fragments des mitochondrialen Gens Cytochrom b) in Kooperation mit WERNER MAYER und SILKE SCHWEIGER bestimmt (SCHULTE et al. 2011b). Im Rahmen der Probennahme wurden Eckdaten (Lebensraum, Jahr der Entdeckung) zur Historie aller Vorkommen zusammengetragen sowie Populationsgrößen geschätzt. Die Schätzung der Populationsgrößen erfolgte über ein langsames Abschreiten des Lebensraums unter Zählung aller adulten Individuen. Unter der Annahme, dass es sich bei der Methode um etwa ein Viertel des tatsächlichen Bestandes handelt, wurde die absolute Populationsgröße mit Hilfe eines Korrekturfaktors hochgerechnet (LAUFER 1998).

Ergebnisse

Herkunft allochthoner Populationen

Es konnten insgesamt acht verschiedene genetische Linien innerhalb der allochthonen Vorkommen in Deutschland nachgewiesen werden. Die Angaben zur natürlichen Verbreitung dieser genetischen Linien beruhen auf den Ergebnissen einer arealweiten Studie von SCHWEIGER et al. (eingereicht) am Naturhistorischen Museum Wien, die vor allem auf Sequenzdaten mitochondrialer Gene beruht, unter Berücksichtigung von Färbungs- und Zeichnungsmustern. Die Linien im Sinne genetisch differenzierter Populationsgruppen entsprechen nicht in allen Fällen den bekannten Unterarten der Mauereidechse. So finden sich teilweise mehrere Linien in validen Unterarten sowie umgekehrt zwei ehemals getrennte Unterarten in einer Linie. Wir verwenden an dieser Stelle jedoch die Zuordnung von Gründerindividuen/Populationen zu einer bestimmten Linie, um deren geografische Herkunft möglichst exakt anzugeben. Absteigend nach ihrer Häufigkeit wurden folgende genetische Linien nachgewiesen:

1) Das natürliche Areal der Südalpen-Linie ist auf das westliche Oberitalien, die Südalpen und das Inntal beschränkt. Diese Linie entspricht der Westform der Unterart *P. m. maculiventris* (SCHULTE et al. 2008, DEICHSEL et al. 2011). Während die Südalpen-Linie innerhalb Deutschlands einzig im ostbayerischen Oberaudorf heimisch ist, tritt sie invasiv weiträumig innerhalb Deutschlands, einschließlich des Nordens auf (Tab. 1, Abb. 1). Die Gründerindividuen dieser Populationen stammen häufig aus der oberitalienischen Seenregion (Gardasee, Lago Maggiore).

2) Die Ostfranzösische Linie ist in Südwestdeutschland, der Westschweiz und dem östlichen Frankreich verbreitet. Eine Unterlinie dieser Populationsgruppe findet sich im Süden Frankreichs (Languedoc). Mauereidechsen der Ostfranzösischen wie auch der Westfranzösischen Linie werden heute einheitlich der Unterart *brongniardii* zugeordnet (SCHULTE et al. 2008). Die frühere Unterteilung ostfranzösischer und westfranzösischer Mauereidechsen in die Unterarten *merremius* bzw. *brongniardii* wurde aufgehoben (SCHWEIGER et al. eingereicht). Das invasive Areal der Ostfranzösischen Linie wirkt wie eine Fortsetzung des natürlichen südwestdeutschen Areals, welches auf Höhe der Linie Bonn–Aachen endet. Eine deutliche Häufung von Populationen diesen Ursprungs lässt sich im Ruhrgebiet erkennen (Abb. 1) und könnte mit einer Weiterverschleppung von Individuen zusammenhängen.

3) Die Venetien-Linie besiedelt die östliche Poebene und Venetien sowie angrenzend Istrien. Diese Linie charakterisiert die östliche Form der Unterart *P. m. maculiventris* (SCHULTE et al. 2008). Bei den eingeschleppten Vorkommen handelt es sich wahrscheinlich um natürliche Hybride zwischen der Toskana- und Venetien-Linie aus der Region Bologna–Modena, die morphologische Charakteristika der Toskana-Linie zeigen, aber basierend auf der mtDNA der Venetien-Linie angehören (S. SCHWEIGER schriftl. Mitt.). Eingeschleppte Populationen dieser Linie finden sich weiträumig verteilt in Deutschland (Tab. 1, Abb. 1).

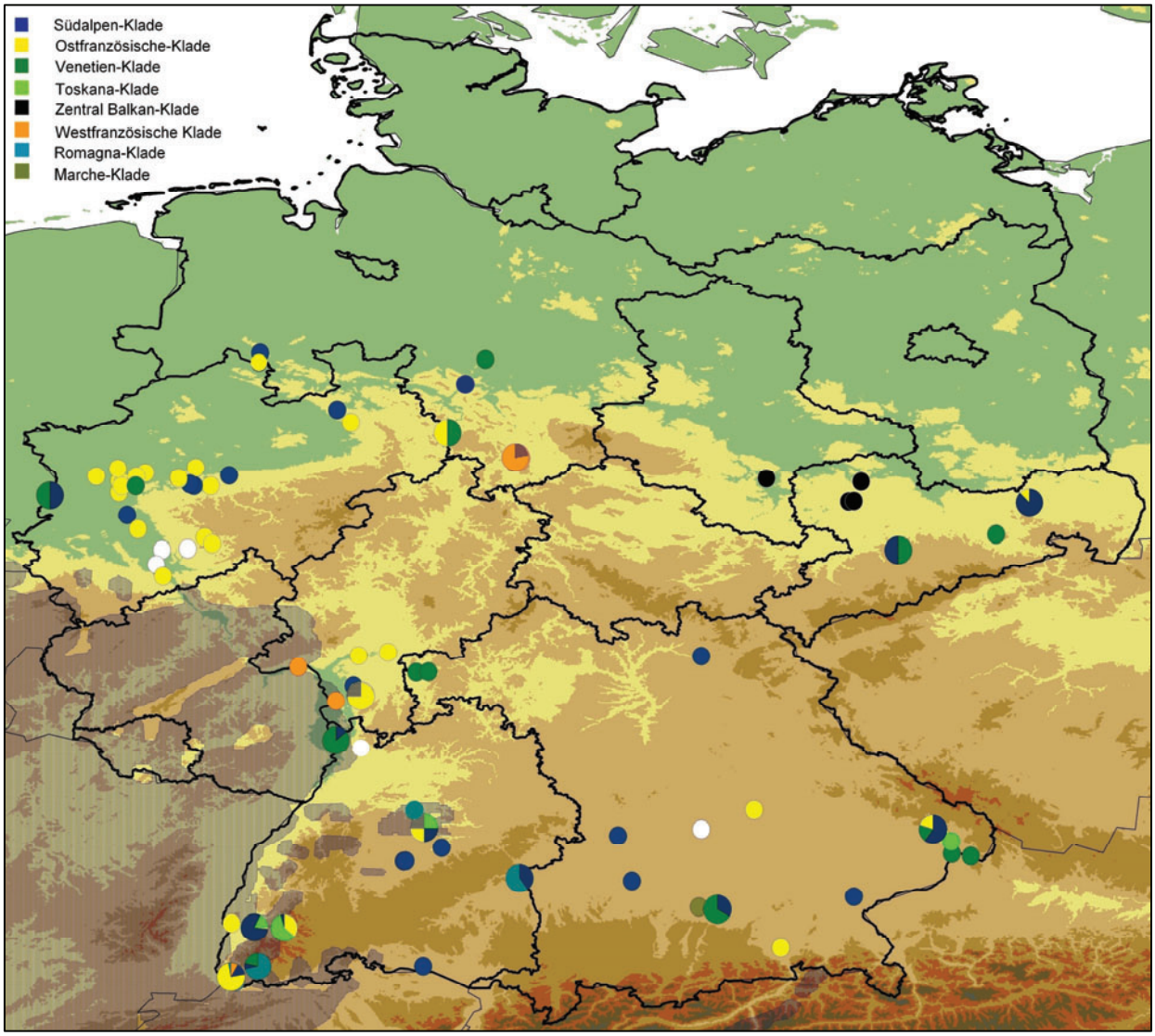

Abb. 1: Verbreitung und Herkunft eingeschleppter Mauereidechsen-Populationen in Deutschland. Weiße Punkte repräsentieren Vorkommen unbekannter Herkunft, schraffierte Anteile in gelben Punkten die Unterlinie Languedoc der Ostfranzösischen Linie, schraffierte Anteile in orangefarbenen Punkten entsprechen dem Vorkommen von *Podarcis liolepis*. Die schraffierte dunklere Fläche im Südwesten Deutschlands sowie im Südosten Bayerns entspricht dem Nordrand des natürlichen Verbreitungsareals der Art.

Distribution and geographic origin of introduced wall lizard populations in Germany. White dots represent populations of unknown origin, shaded fractions within yellow dots represent the Subclade Languedoc of the eastern France lineage, shaded fractions within orange dots represent *P. liolepis*. The dark shaded area in south-western Germany and south-eastern Bavaria corresponds to the northern range margin of the species' native range.

4) Die Toskana-Linie, die in der Region Latium und der Toskana verbreitet ist. Morphotypen dieser Linie finden sich allerdings sowohl in Ligurien als auch in der Emilia-Romagna und legen eine natürliche Hybridisierung mit benachtbarten Linien nahe (S. SCHWEIGER schriftl. Mitt.). Die Toskana-Linie entspricht der morphologisch gut fassbaren Unterart *P. m. nigriventris*. Diese Linie ist weniger häufig und ausschließlich im Süden Deutschlands innerhalb eingeschleppter Populationen zu finden (Tab. 1, Abb. 1). Natürliche Hybride aus der Kontaktzone der Toskana- und Südalpen-Linie in Ligurien wurden früher als Unterart *brueggemanni* (Terra typica: La Spezia) bezeichnet. Diese Mauereidechsen sind grün gefärbt und kleinfleckig gezeichnet.

5) Die Romagna-Linie besiedelt ein Areal in der Region Emilia-Romagna. Haplotypen dieser Linie konnten im natürlichem Areal der Mauereidechse im äußersten Südwesten Deutschlands im deutsch-schweizerischem Grenzgebiet sowie in Ulm und im Kreis Ludwigsburg nachgewiesen werden.

6) Die Zentral-Balkan-Linie ist in Ostösterreich und dem zentralen Balkan bis Bulgarien verbreitet. Sie entspricht der Nominatform *P. m. muralis*. Insbesondere an den invasiven Vorkommen der Zentral-Balkan-Linie wird der vermutlich große Einfluss menschlicher Reisebewegungen auf die Einschleppungen deutlich. So konnte diese Linie ausschließlich in den neuen Bundesländern (Sachsen-Anhalt und Sachsen, Tab. 1, Abb. 1) nachgewiesen werden. Der Aussetzungszeitpunkt und die Herkunft der Populationen legen nahe, dass die Gründerindividuen der Vorkommen aus Ungarn stammen. Ungarn war ein beliebtes Reiseziel für Bürger der DDR und die Haplotypen der Populationen sind beinahe identisch zu denen von Tieren aus Ungarn. Die Ergebnisse erinnern stark an Fälle der Europäischen Sumpfschildkröte (FRITZ et al. 2004), bei der die Herkunft zahlreicher Individuen in Südwestdeutschland, und im Gegensatz zum östlichen Deutschland, häufige unterschiedliche menschliche Reiserouten widerspiegelt.

7) Die Westfranzösische Linie ist eine in Westfrankreich und den östlichen Pyrenäen verbreitete Linie. Diese Linie ist der Unterart *P. m. brongniardii* zugehörig und konnte innerhalb von Populationen in Lörrach, im westlichen Rhein-Main-Gebiet sowie in Südniedersachsen nachgewiesen werden (Tab. 1, Abb. 1).

8) Auf die Marche-Linie, verbreitet in der mittelitalienischen Region Marche (Ancona und weitere Umgebung) sowie in Westistrien, geht in Deutschland ein Vorkommen im Stadtgebiet von München zurück.

Tafel 1: Obere Reihe: Südalpen-Linie. Von links: Männchen dorsal und ventral (Ueffeln, Standort 1), Weibchen dorsal und ventral (Ueffeln, Standort 1). Untere Reihe: Ostfranzösische Linie. Von links: Männchen dorsal und ventral (Duisburg Innenhafen, Standort 21), Weibchen dorsal und ventral (Lörrach, Standort 61). Fotos: U. SCHULTE.

Upper row: Southern Alps lineage. From left: dorsal and ventral view of a male (Ueffeln, locality 1), dorsal and ventral view of a female (Ueffeln, locality 1). Lower row: Eastern France lineage. From left: dorsal and ventral view of a male (Duisburg basin, locality 21), dorsal and ventral view of a female (Lörrach, locality 61).

Tafel 2: Obere Reihe: Venetien-Linie. Von links nach rechts: Männchen dorsal und ventral (Mannheim, Standort 46), Weibchen dorsal und ventral (Hannover, Standort 3). Untere Reihe: Toskana-Linie. Von links nach rechts: Männchen dorsal und ventral (Schärding, Österreich), Weibchen dorsal und ventral (Schärding, Österreich). Fotos: U. SCHULTE.

Upper row: Venetian lineage. From left to right: dorsal and ventral view of a male (Mannheim, locality 46), dorsal and ventral view of a female (Hannover, locality 3). Lower row: Tuscany lineage. From left to right: dorsal and ventral view of a male (Schärding, Austria), dorsal and ventral view of a female (Schärding, Austria).

Tafel 3: Obere Reihe: Zentral-Balkan-Linie. Von links nach rechts: Männchen dorsal und ventral (Ammelshain, Standort 35), Weibchen dorsal und ventral (Ammelshain, Standort 35). Untere Reihe: Westfranzösische Linie. Von links nach rechts: Männchen dorsal und ventral (Nörten-Hardenberg, Standort 5), Weibchen dorsal und ventral (Gernsheim, Standort 44). Fotos: U. SCHULTE.

Upper row: Central Balkan lineage. From left to right: dorsal and ventral view of a male (Ammelshain, locality 35), dorsal and ventral view of a female (Ammelshain, locality 35). Lower row: Western France lineage. From left to right: dorsal and ventral view of a male (Nörten-Hardenberg, locality 5), dorsal and ventral view of a female (Gernsheim, locality 44).

Tafel 4: Obere Reihe von links: Romagna-Linie. Männchen dorsal und ventral (Inzlingen, Standort 63). Weibchen dorsal und ventral (Inzlingen, Standort 63). Untere Reihe von links: Marche-Linie. Männchen dorsal und ventral (München-Aubing, Standort 79), Hybrid zwischen der Toskana-, Südalpen- und Ostfranzösischen-Linie. Weibchen dorsal und ventral (Freiburg Dreisam, Standort 59). Fotos: U. SCHULTE (obere Reihe und untere Reihe Hybriden); J. GEBHART (untere Reihe Marche-Linie).

Upper row from left: Romagna lineage. Dorsal and ventral view of a male (Inzlingen, locality 63), dorsal and ventral view of a female (Inzlingen, locality 63). Lower row from left: Marche lineage. Dorsal and ventral view of a male (München-Aubing, locality 79), Hybrid between Tuscany, Southern Alps and Eastern France lineages. Dorsal and ventral view of a female (Freiburg Dreisam, locality 59).

Die mit Abstand meisten eingeschleppten Populationen in Deutschland (80,9 %) gehen auf Gründerindividuen der Südalpen-, der Ostfranzösischen und der Venetien-Linie zurück (Tab. 1). Die natürliche Verbreitung der Südalpen- sowie die Ostfranzösischen Linie stellt die nordwestliche Arealgrenze der Art dar. Aufgrund einer relativ großen Überlappung der klimatischen Bedingungen ihres natürlichen Areals mit dem Aussetzungsraum sind diese genetischen Linien vermutlich bereits vorangepasst und unter anderem wohl deshalb häufig innerhalb eingeschleppter Populationen vertreten (SCHULTE et al. 2011b). Ein Vergleich der klimatischen Bedingungen im natürlichen und invasiven Areal der Zentral-Balkan-Linie zeigt, dass diese an weitaus tiefere Wintertemperaturen angepasst ist, als es in ihrem neuen Areal im östlichen Deutschland der Fall ist. Die Etablierung zentralitalienischer Linien (Marche-, Toskana- sowie Romagna-Linie) nördlich der Alpen zeigt die erstaunliche Breite der Klimanische der Art an, sie könnte jedoch auch auf einer Aussetzung innerhalb spezieller Gunsträume beruhen. In einer Population der Westfranzösischen Linie in Südniedersachsen konnte ein für Deutschland bisher unbekanntes Neozoon nachgewiesen werden: die Katalonische Mauereidechse (*Podarcis liolepis*) aus dem Artenkomplex der Iberischen Mauereidechse (RENOULT et al. 2010, SCHULTE et al. eingereicht).

Tab. 1: Häufigkeit der acht verschiedenen genetischen Linien innerhalb eingeschleppter und molekulargenetisch analysierter Mauereidechsen-Vorkommen in Deutschland (n = 77). Mehrere Haplotypen in Populationen wurden einzeln ausgewertet.

Frequency of eight distinct genetic lineages within introduced and an-alysed wall lizard populations in Germany (n = 77). Multiple haplotypes within populations were analysed separately.

Linie	Anteil (%) innerhalb der 77 Vorkommen
Südalpen	34,8
Ostfranzösische	31,5
Ostfranzösische (Languedoc)	2,2
Venetien	12,4
Toskana	4,5
Romagna	4,5
Zentral-Balkan	4,5
Westfranzösische	4,5
Marche	1,1

Mehrfacheinschleppungen

In 15 allochthonen Populationen konnten Mehrfacheinschleppungen von Mauereidechsen unterschiedlicher Herkunft nachgewiesen werden (SCHULTE et al. 2011b). Berücksichtigt man ausschließlich die 43 Populationen, in denen mehr als ein Individuum analysiert wurde, so basieren etwa 35 % der Populationen aus Gründerindividuen unterschiedlicher Herkunftsregionen. Dies lässt vermuten, dass ein höherer Stichprobenumfang pro Population weitaus mehr Mehrfacheinschleppungen aufdecken würde. Insbesondere in größeren individuenstarken Populationen sollten aus diesem Grund zur Herkunftsbestimmung mindestens 5–10 Individuen beprobt werden (MUIRHEAD et al. 2008).

Tab. 2: Allochthone Mauereidechsen-Vorkommen in Deutschland (Stand: 25.8.2011). *n* = Anzahl genetisch untersuchter Individuen. Introduced wall lizard populations in Germany (as of 25.8.2011). *n* = number of analysed specimens.

Lage	Lebensraum	Vermutlicher Ursprung/ Jahr der Entdeckung	Bestandsgröße	*n*	Herkunft/ genetische Linie	Bemerkungen zu Hybridisierungen oder Interaktionen
Niedersachsen						
1. Ueffeln	Steinbruch, Heide	Aussetzung 1979	300 Ind.	2	Südalpen-Linie	Sympatrie mit Zauneidechsen
2. Osnabrück	Botanischer Garten	Aussetzung	50 Ind.	2	Ostfranzösische Linie	
3. Hannover	Herrenhäuser Gärten	Aussetzung	50 Ind.	3	Venetien-Linie	
4. Springe	Steinbruch	Aussetzung	20-30 Ind.	3	Südalpen-Linie	
5. Nörten-Hardenberg	Ruine, Gemäuer, Fels	Aussetzung, Ende der 1980er Jahre	*muralis* = 600 Ind. *liolepis* = 150 Ind.	11	Westfranzösische Linie (südl. Pyrenäen)	Sympatrie mit Zauneidechsen
Nordrhein-Westfalen						
6. Bielefeld-Quelle, Ostwestfalendamm	felsiger Hang (Kalkstein)	Aussetzung, 1996 entdeckt	etwa 70-100 Ind.	1	Südalpen-Linie	
7. Schloss-Holte-Stukenbrock	Bahnhof und Umgebung	entflohene Terrarientiere, 1964	etwa 300-500 Ind.	2	Ostfranzösische Linie	Sympatrie mit Zauneidechsen
8. Stahle (Rötanschnitt)	Steilhang im Röt	Aussetzung, 1991 entdeckt	etwa 30-50 Ind.	2	Ostfranzösische Linie Venetien-Linie	Sympatrie mit Zauneidechsen
9. Holzwickede	Bahnanlage Böschung, im April 2007 Einebnung	Aussetzung, 2002 entdeckt	nach Habitatzerstörung 04.2007: 10-20 Ind.	1	Südalpen-Linie	
10. Dortmund (Hengsteysee)	Schieferfelshänge und Garten	Aussetzung, 1987 und in den 1950er Jahren entdeckt	über 200 Ind.	2	Ostfranzösische Linie	Sympatrie mit Zaun- und Waldeidechsen
11. Castrop-Rauxel	Zechengelände Erinpark , Mauern	Aussetzung, 2005 entdeckt	über 100 Ind.		u. a. Tiere von der Ahr	
12. Witten-Heven	Böschungsmauer (Ruhrsandstein) am Fuß des Ruhrhang, Gartengelände	Aussetzung ca. 2004	zwischen 40 und 100 Ind.	3	Südalpen-Linie	
13. Witten-Bommern	Trockenmauer	Aussetzung	etwa 100 Ind.	1	Südalpen-Linie	Sympatrie mit Zauneidechsen
14. Bochum, S-Bahnhof Ehrenfeld	Bahnanlage	Aussetzung, 2002 entdeckt	etwa 10 Ind.	k. A.	Ostfranzösische Linie	
15. Bochum Botanischer Garten	Alpinum	Aussetzung, 1995 entdeckt	etwa 20 Ind.	2	Ostfranzösische Linie	
16. Bottrop-Batenbrock	Bergehalde	Aussetzung, seit 2006 bekannt	etwa 30	3	Ostfranzösische Linie	
17. Dinslaken-Süd	Halde,, Schlackengelände, vegetationsarme Kuppe	Aussetzung, 1999 entdeckt	über 200 Ind.	1	Ostfranzösische Linie	
18. Mühlheim a. d. R.	Sandsteinbruch	Aussetzung, 2003 entdeckt	etwa 50 Ind.	2	Venetien-Linie	Sympatrie mit Zauneidechsen
19. Oberhausen-Neue-Mitte	Sandsteinmauer (Gabionenwand) und Uferschüttung	Aussetzung, 2003 entdeckt	nur wenige Ind., 10 Ind.	1	Ostfranzösische Linie	
20. Duisburg-Ruhrort Hafen	Dammböschung der Ruhr, Bruchstein/Rasengittersteine	Aussetzung, 2004 entdeckt	über 150 Ind.	1	Ostfranzösische Linie	
21.Duisburg Innenhafen	Befestigungsmauer des Hafenbeckens	Aussetzung, 1987 entdeckt	etwa 50	3	Ostfranzösische Linie	
22. Duisburg-Hochfeld	Befestigungsmauern, Bahndamm	Aussetzung, 2007 entdeckt	etwa 20-30	2	Ostfranzösische Linie	
23. Duisburg-Hüttenheim	Schlackengelände	12 entflohene Terrarientiere, 1978	≥ 8 Ind. (2000)	1	Ostfranzösische Linie	
24. Kamp-Lintfort	Halde	Aussetzung	k. A.	1	Ostfranzösische Linie	
25. Nettetal-Kaldenkirchen	Bahndamm	Güterverkehr? mind. 2004	etwa 50-100 Ind.	2	Südalpen-Linie	Sympatrie mit Zauneidechsen
26. Düsseldorf	Botanischer Garten	Aussetzung	etwa 60-100 Ind.	1	Südalpen-Linie	
27. Monheim	Bahnanlage	Aussetzung, 2003 entdeckt, zunehmende Ausdehnung (BÖHM) auf 1 km Länge	über 150 Ind.	3	Ostfranzösische Linie	Sympatrie mit Zauneidechsen
28. Remshagen	Abgrabung	Aussetzung, seit etwa 1980 bekannt	etwa 50 Ind.	2	Ostfranzösische Linie	
29. Weiershagen	Steinbruch	Aussetzung, 2005 entdeckt	etwa 30 Ind.	3	Ostfranzösische Linie	Sympatrie mit Zauneidechsen
30. S-Bahn Köln-Overath, Höhe Rennweg	Bahndamm / Holzunternehmen	vermutl. über Holzlieferungen eingeschleppt 1970er Jahre	etwa 20 Ind. abnehmend		unbekannt, auffällig dunkle Tiere	
31. Köln-Rath	Gleisanlage	Seit 2003 bekannt, möglichereweise erloschen (2009)	etwa 20-40 Ind.		k. A.	Sympatrie mit Zauneidechsen
32. Niederkassel-Lülsdorf	Basaltmauer Rheinufer	Seit ca. 1980 bekannt, nach 1990 verschollen. Ggf. neu ausgesetzte Tiere seit 2008	k. A.		k. A.	
33. Bonn-Poppelsdorf (Botanische Gärten)	Mauern, Biotopanlage, Trockenbiotop	Aussetzung, Tiere von der Ahr, 1999 (< 10 Ind.)	etwa 60 Ind., expandierend	1	Ostfranzösische Linie	
Sachsen-Anhalt						
34. Halle (Botanischer Garten)	Alpinum und Begrenzungsmauern zur Stadt	ausgesetzt oder aus Haltung entwichen, 2006	etwa 40 Ind.	2	Zentral-Balkan-Linie	
Sachsen						
35. Ammelshain	NSG „Porphyr Steinbruch	Aussetzung, 1980er	über 1000 Ind.	1	Zentral-Balkan-Linie	Sympatrie mit Zauneidechsen

Lage	Lebensraum	Vermutlicher Ursprung/ Jahr der Entdeckung	Bestandsgröße	*n*	Herkunft/ genetische Linie	Bemerkungen zu Hybridisierungen oder Interaktionen
	Haselberg“	Jahre				
36. Altenhain		Sekundärverschleppung von Pop. 35., oder Expansion	etwa 200	2	Zentral-Balkan-Linie	Sympatrie mit Zauneidechsen
37. Frankenberg	Böschung und Treppe der Autobahnbrücke	Aussetzung	etwa 40 Ind.	2	Südalpen-Linie Venetien-Linie	
38. Böhlitz	Steinbruch Holzberg Böhlis	Sekundärverschleppung von Pop. 35?			Zentral-Balkan-Linie	
39. Dresden-Loschwitz	Hausmauern in der Stadt, Loschwitzer Elbhänge	Aussetzung um 1900	über 200 Ind.	2	Venetien-Linie	
40. Kamenz	Felshang und Mauerwerk vom Friedhof	Aussetzung, 1970-1980er Jahre	150-200 Ind., isoliert,	8	Südalpen-Linie Ostfranzösische Linie	
Hessen						
41. Frankfurt	Hauptgüterbahnhof	Aussetzung oder Güterverkehr? seit 1997	etwa 200-250 Ind.	1	Ostfranzösische Linie	
42. Darmstadt	Rangierbereich, Hauptbahnhof	Güterverkehr? 2004		1	Südalpen-Linie	
43. Darmstadt-Eberstadt	NSG „Bessunger Kiesgrube“, Steinhalde, Felswände, Böschungen	Aussetzung, 2003	etwa 200	4	Ostfranzösische Linie Ostfranzösische Linie (Languedoc)	Sympatrie mit Zauneidechsen
44. Gernsheim	Bahnhof, Ruderalfläche und Friedhof	Aussetzung oder Güterverkehr, 1989	über 200	2	Westfranzösische-Linie	Sympatrie mit Zauneidechsen
Rheinland-Pfalz						
45. Mainz (Budenheim)	Steinbruch	Umsiedlung		3	Westfranzösische-Linie	
Baden-Württemberg						
46. Mannheim	Riedbahnbrücke	Aussetzung	640 Ind.	49	Venetien-Linie Südalpen-Linie	Hybridisierung mit heimischen Mauereidechsen
47. Mannheim Suebenheim	ehemaliges Airbase Gelände	durch Expansion von Pop. 46 entstanden				Hybridisierung mit heimischen Mauereidechsen
48. Dossenheim	Neckarufer	Vermutliche Satellitenpopulation von Pop. 46	über 100 Ind.			Sympatrie mit Zauneidechsen
49. Kreis Ludwigsburg	Mauerwerk	Unbekannt, vermutlich Aussetzung		2	Romagna-Linie	vermutlich Hybridisierung mit heimischen Mauereidechsen
50. Stuttgart Kriegsberg/Mönchhalde/Fraunhoferstr	Gärten, Weinberge	Aussetzung von 12 Indi. aus Wildberg a.d. Nabold, 1874 durch Prof. Jäger	über 500 Ind.	2	Ostfranzösische Linie	
51. Stuttgart West	(Ex-) Bahngelände, Expansion in Gärten, zum Birkenkopf	Güterverkehr		4	Südalpen-Linie	
52. Stuttgart in/um zool./bot. Garten Wilhelma	Parkanlagen	multiple Aussetzungen in den 1970-er Jahren	etwa 200 Ind.	9	Toskana-Linie Südalpen-Linie	
53. Stuttgart Tavertinpark	ehemaliger Steinbruch	multiple Aussetzungen		3	Ostfranzösische Linie (normal, Languedoc) Südalpen-Linie	
54. Stuttgart Bad Canstatt, Wangen, Untertürkheim	Ruderalgelände, Neckarufer, (Ex-) Bahngelände	Güterverkehr Multiple Verschleppungen		7	Ostfranzösische Linie (normal, Languedoc) Südalpen-Linie	
55. Nürtingen	Böschung	Aussetzung 1991, 11 Ind. vom Gardasee	etwa 200	3	Südalpen-Linie	Syntopie mit Zauneidechsen
56. Tübingen	Spitzberg (Fels) und Schlossmauern	Aussetzung von Tieren aus Bozen durch Prof. Eimer vor 1889	über 500 Ind.	1	Südalpen-Linie	
57. Tübingen Innenstadt Parkhaus König	Gabionen, Gärtnerei, Mauern	Umsiedlung vom Schloss 1982 (Deichsel & Rutschke)	über 200 Ind.	1	Südalpen-Linie	
58. Ulm	Kleingartengelände Galgenberg, Adlerbastei	Güterverkehr, multiple Aussetzungen? mindestens seit 1946, Expansion donauabwärts	Galgenberg: etwa 1000 Adlerbastei : etwa 100	5	Adlerbastei: Südalpen-Linie Galgenberg: Romagna-Linie	
59. Freiburg Dreisam	Flussufer Dreisam	multiple Aussetzungen, erste grünrückige 1960er Jahre	450 Ind.	52	Südalpen-Linie Toskana-Linie Ostfranzösische Linie	Hybridisierung mit heimischen Mauereidechsen
60. Freiburg Messe	Messegelände, Güterbahnhof	Güterverkehr? „rollende Autobahn“	275 Ind.	22	Toskana-Linie Ostfranzösische Linie Südalpen-Linie	Hybridisierung mit heimischen Mauereidechsen
61. Kaiserstuhl (Ihringen)	Südspitze des Winklerbergs (Fels)	Aussetzung 1994-1999			Jungtiere von Mittelrhein und Mosel	
62. Lörrach-Stetten	Flussufer Wiese	Einwanderung aus basel-Riehen,, dort primär Güterverkehr oder Aussetzung	800 Ind.	71	Südalpen-Linie Romagna-Linie Ostfranzösische Linie Westfranzösische Linie	Hybridisierung mit heimischen Mauereidechsen Syntopie mit Zauneidechsen
63. Inzlingen	Gartengelände, Brachflächen	Einwanderung aus Basel-Riehen, dort primär Güterverkehr oder Aussetzung	160 Ind.	14	Romagna-Linie Venetien-Linie Südalpen-Linie	Hybridisierung mit heimischen Mauereidechsen
64. Mainau	Insel Mainau, Bot. Garten	Aussetzung oder Transport mit Pflanzen	über 1000 Ind.	2	Südalpen-Linie	
Bayern						
65. Pompejanum Aschaffenburg	Ruine, archäologischer Park	Aussetzung, vor 1966	über 250 Ind.	1	Venetien-Linie	
66. Aschaffenburg	Bahnhof	Satellitenpop. vom Pompejanum		3	Venetien-Linie	
67. Kulmbach	Güterbahnhof	Güterverkehr?	über 250 Ind.	3	Südalpen-Linie	

Lage	Lebensraum	Vermutlicher Ursprung/ Jahr der Entdeckung	Bestandsgröße	*n*	Herkunft/ genetische Linie	Bemerkungen zu Hybridisierungen oder Interaktionen
68. Kelheim	stillgelegte Gleisanlage, Siedlungsgebiet	Güterverkehr, ca. 1997, Expansion	etwa 1000 Ind.	1	Ostfranzösische Linie	Sympatrie mit Zauneidechsen
69. Ingolstadt	Bahnanlage					
70. Donauwörth	Bahnanlage	Güterverkehr?, ca. 2003	über 500 Ind.	1	Südalpen-Linie	
71. Augsburg	Bahnanlage		über 110 Ind.	1	Südalpen-Linie	
72. Tittling	Bahnanlagen	Aussetzung	100-200 Ind.	5	Ostfranzösische Linie Südalpen-Linie Venetien-Linie	
73. Hutthurm	Bahnanlagen	Güterverkehr oder Aussetzung	10-20 Ind.	1	Toskana-Linie	
74.-77. Passau - Erlautal – Obernzell - Jochenstein	Veste Oberhaus, Trockenmauern, Ruine Hals, Grubweg, Donauleiten übers erlautal bis Jochenstein	Aussetzung 1932, danach weitere Aussetz-ungen, ausgebreitet auf 25 km Länge,	4.000-6.000	4	Venetien-Linie	Sympatrie mit Zauneidechsen
78. Eisenfelden	Gebäuderuine, Bahnhof	vor 2000	über 50 Ind.	2	Südalpen-Linie	
79. München Aubing	Bahnanlage, Hang	Güterverkehr? mindestens 2007	über 100 Ind.	1	Marche-Linie	
80. Südbahnhof München	Güterbahnhof	Güterverkehr? mindestens 1999	über 100 Ind.	1	Südalpen-Linie	
81. Laim-Donnerberger Brücke	Eisenbahnlinie	Güterverkehr? 1987-1997	über 100 Ind.	3	Südalpen-Linie Venetien-Linie	Sympatrie mit Zauneidechsen
82. Rosenheim - Kolbermoor	Bahnlinie, Aicher Park Betriebsgelände	unbekannt	etwa 200 Ind.	2	Ostfranzösische Linie	Hinweis: der autochthoner Bestand der Südalpen-Linie liegt 25 km entfernt in Oberaudorf

Eine Vermischung unterschiedlicher Ursprungspopulationen aus dem Kernareal einer Art führt häufig zu einer Erhöhung der genetischen Diversität als Grundlage für Anpassungsprozesse innerhalb invasiver Populationen (z. B. bei *Anolis sagrei*; KOLBE et al. 2004, KOLBE et al. 2008) und ist auch innerhalb ausgewählter langjährig etablierter Mauereidechsen-Populationen zu beobachten (SCHULTE et al. unveröff.). Am häufigsten fanden sich Mischpopulationen, die sich aus Gründerindividuen der Südalpen- und Venetien-Linie zusammensetzen. DEICHSEL et al. (2011) beschreiben die Situation von Mehrfacheinschleppungen im Stadtgebiet Stuttgart. Zahlreiche Populationen desselben Ursprungsgebietes in unmittelbarer Umgebung (z. B. Duisburg, Witten und Ammelshain) deuten auf mögliche Folgeaussetzungen von Individuen durch den Menschen oder auf Verschleppung durch Güterverkehr hin.

Autochthon oder allochthon? – Eine nicht-genetische Entscheidungshilfe

Eine molekulargenetische Determination potenziell gebietsfremder Mauereidechsen erlaubt eine schnelle und sichere Aussage, ob der Verdacht einer Einschleppung begründet ist und woher die betroffenen Tiere stammen. Ein molekulargenetisches Labor steht nur in wenigen Fällen zur Verfügung, und der Einsatz von Naturschutzmitteln für molekulargenetische Untersuchungen sollte gut begründet sein. Im Folgenden bieten wir daher eine morphologische Orientierungshilfe zur Beurteilung einer potenziellen Einschleppung, aufgrund derer für oder gegen eine molekulargenetische und damit eindeutige Determination entschieden werden kann. Die hohe innerartliche Färbungs- und Zeichnungsvariabilität der Mauereidechse, die auch innerhalb und zwischen Populationen ein und derselben evolutionären Linie stark ausgeprägt sein kann (BELATTI et al. 2011), erschwert die Zuordnung von Vorkommen zu einer bestimmten Herkunftsregion anhand von Einzelindividuen. So sind eingeschleppte Individuen und insbesondere Hybride derselben innerhalb natürlicher Vorkommen auf rein morphologischer Basis nicht sicher zu erkennen. Eine Ausnahme bilden die zentralitalienischen Linien (Marche, Romagna, Toskana) sowie die Venetien-Linie aus dem Raum Bologna–Modena, die teilweise eine grüne Rückenfärbung

aufweisen. Alle übrigen Linien sind – wenn überhaupt – über ihre Bauchfärbung und -zeichnung zu unterscheiden. Im Folgenden wird daher versucht, morphologische Unterscheidungsmerkmale zwischen den einzelnen Linien herauszuarbeiten, die eine Identifikation im Feld zulassen (vgl. Tafeln 1–4).

Die Rückenfärbung heimischer Mauereidechsen der Ostfranzösischen Linie (*P. m. brongniardii*) schwankt im gesamten südwestdeutschen Areal zwischen hell- bis mittelbraun und grau. Grüntöne fehlen völlig. Bauchseite und Kehle sind häufig weißlich, gelblich, orange oder rötlich gefärbt und relativ schwach gefleckt. Insgesamt sind Individuen der Ostfranzösischen Linie deutlich kleiner als Individuen der übrigen Linien. Die Südalpen-Linie, die in Deutschland autochthon ausschließlich in zwei Populationen im bayerischen Oberaudorf vorkommt, ist ventral gelblich bis ockerfarben und orangebraun gefärbt und zeigt als gutes Unterscheidungsmerkmal zur Ostfranzösischen Linie eine deutliche schwarze (teilweise auch orange) Fleckung der Kehle und Bauchseite (SCHULTE 2008, Tafel 1). Die in Deutschland invasiv auftretende Venetien-Linie zeigt morphologische Charakteristika von Individuen der Unterart *P. m. nigriventris*. Dazu gehören eine grüne, teilweise aber auch bräunliche Rückenfärbung sowie eine deutliche Schwarzfleckung der stets weißen Unterseite. Die Kopfregion von Individuen dieser Linie ist deutlich dunkler gefärbt, als die heimischer Mauereidechsen. Die zuvor genannten Charakteristika entsprechen mehr oder weniger ebenfalls denen weiterer italienischer Linien (Toskana-Linie, Romagna-Linie und Marche-Linie), wobei Individuen der Romagna und Marche-Linie häufig auch braunrückig sein können. Die schwarzgrüne Retikulierung des Rückens sowie eine nach Süden klinal zunehmende Schwarzfleckung der Unterseite (GRUSCHWITZ & BÖHME 1986) sind bei der Toskana-Linie besonders stark ausgeprägt. Zudem handelt es sich bei dieser Linie um die größten und kräftigsten Mauereidechsen.
Die Westfranzösische Linie wird größer als die Ostfranzösische Linie und zeigt bei ähnlicher Grundfärbung deutlichere Zeichnungsmuster (Längsstreifung, Pigmentierung und Fleckung der Unterseite). Morphologisch am schwierigsten fassbar ist die Zentral-Balkan-Linie, deren Individuen oberseits wie heimische Mauereidechsen braun, braungrau oder grau, niemals aber grün gefärbt sind. Die Unterseite ist meist weißlich, orange oder rötlich (nie gelblich) und bei den Männchen vor allem an der Kehle schwarz gefleckt.

Aufgrund der unterschiedlichen Häufung eingeschleppter Linien sollte bei der Feldarbeit in erster Linie auf eine Unterscheidung der Ostfranzösischen, der Südalpen und der Venetien-Linie geachtet werden. Im Gegensatz zu den Schwierigkeiten einer phänotypischen Zuordnung potenziell eingeschleppter Populationen erlaubt das gut dokumentierte autochthone Verbreitungsareal der Mauereidechse in Deutschland eine sichere Trennung zwischen natürlichen und allochthonen Vorkommen, es sein denn, eine vermeintliche Ausbürgerung erfolgte innerhalb des natürlichen Areals.

Aussetzungen von Mauereidechsen – ein naturschutzfachliches Problem

Schon Ende des 19. und Anfang des 20. Jh. wurden Mauereidechsen in Deutschland ausgesetzt (DÜRIGEN 1897, MERTENS 1917). Wir können davon ausgehen, dass bis heute die Gründe, Mauereidechsen auszusetzen, sich vor allem auf folgende Überlegungen zurückführen lassen: 1) Neugierde auf ein »Freilandexperiment«, 2) gezielte »Bereicherung« des Standortes durch eine neue Art, 3) die vermeintliche »Stützung von Beständen« durch das Einbringen weiterer Individuen sowie 4) »Entsorgung« eigener Nachzuchten der Art.

Die Aussetzungsgründe überschneiden sich häufig, insbesondere, wenn es um einen neuen, vom Menschen geschaffenen Standort geht (Steinbrüche, Straßenböschungen, Halden, Botanische Gärten, Burg- und Bahnanlagen etc.). Die vielen erfolgreichen Ansiedlungen in geeigneten Lebensräumen dokumentieren den Sachverstand der Urheber, die vornehmlich aus dem Kreis der Terrarianer stammen dürften. Neben diesen gezielten Aussetzungen dürften aber auch unbeabsichtigte Verschleppungen, insbesondere durch den Schienenverkehr vor allem in Süddeutschland, eine Rolle spielen. Dies lässt sich jedoch kaum beweisen, höchstens durch die Herkunft der Tiere (siehe oben) nahelegen.

Aktueller rechtlicher Status und Einstufung des Gefährdungspotenzials

Aussetzungen sowie auch die Haltung gebietsfremder, aber auch heimischer Mauereidechsen, sind nach dem Bundesnaturschutzgesetz (BNatSchG) vom 29 Juli 2009 nach § 40 Absatz 4 ohne eine entsprechende Genehmigung der zuständigen Behörde untersagt. Die Vielzahl der Aussetzungen zeigt aber, dass die Genehmigungspflicht entweder nicht bekannt ist oder bewusst ignoriert wird. Wir müssen davon ausgehen, dass die möglichen negativen Auswirkungen ungenehmigter Aussetzungen den handelnden Personen nicht oder nur unzureichend bekannt sind. Aufgrund der fehlenden Definition der Mauereidechse als invasive Art ist der Umgang nach derzeitigem Recht gemäß § 7 Abs. 2 Nr. 7 BNatSchG geregelt. Demnach würden alle allochthonen Mauereidechsen-Populationen, die sich über »einige« Generationen in der heimischen Natur ohne menschliche Hilfe erhalten konnten (in einer älteren Definition waren dies nur 3 Generationen, GEITER 2003), den gleichen rechtlichen Status genießen wie autochthone Populationen. Bislang wird im Naturschutzrecht sowie teilweise in der Praxis nicht zwischen heimischen und gebietsfremden Unterarten oder genetischen Linien differenziert. Nach Tabelle 2 würde somit ein rechtlicher Schutz auf etwa 41 der 51 Populationen (80,4 %) zutreffen, deren Aussetzungszeitpunkt bekannt ist und die bereits einige Generationen (in diesem Fall über 3 Generationen) ausgebildet haben. In Folge dessen kommt es bereits seit einiger Zeit zu kostenaufwändigen Umsiedlungen allochthoner Populationen, die z. B. von Bauprojekten betroffen sind (z. B. innerstädtische Ruderalflächen, Bahnbereiche). Würde die Mauereidechse aber als »invasive Art« eingestuft, hätte Deutschland nach § 40 Absatz 1 BNatSchG geeignete Maßnahmen zu treffen, um einer von ihnen ausgehenden Gefährdung entgegenzuwirken. Demnach würde nach § 40 Absatz 1, 2 und 3 BNatSchG neben der Prävention die Aufgabe bestehen, bei bereits verbreiteten Populationen eine weitere

Ausbreitung zu verhindern oder die Auswirkungen der Ausbreitung zu vermindern. Generell lassen sich Aussetzungen von Mauereidechsen und ihre Auswirkungen in drei Kategorien einteilen.

1) Aussetzungen innerhalb des natürlichen Areals (Gefährdung der genetischen Integrität autochthoner Populationen).
2) Aussetzungen innerhalb von Lebensräumen mit anderen Eidechsenarten, vor allem der Zauneidechse (potenzielle Verdrängung der Zauneidechse).
3) Aussetzungen an Standorten außerhalb des Gebietes autochthoner Vorkommen und ohne weitere Eidechsenarten (Gefahr der Ausbreitung und späteren Gefährdung anderer Eidechsenarten).

Zu 1) Besonders kritisch sind Aussetzungen von Tieren fremder genetischer Linien innerhalb des natürlichen Areals der Art. Innerhalb von Kontaktzonen in Baden-Württemberg konnte bereits eine weiträumige Hybridisierung zwischen heimischen Mauereidechsen (Ostfranzösische Linie oder *P. m. brongniardii*) und vier italienischen Linien (Südalpen, Toskana, Romagna, Venetien) sowie der Westfranzösischen Linie nachgewiesen werden (SCHULTE et al. unveröff.). Das Resultat ist eine schnelle genetische Assimilation der heimischen Population, wobei aufgrund der Dominanz der italienischen Linien der Genpool der heimischen Unterart eventuell vollkommen verschwindet (gene pool swamping; BARTON & HEWITT 1985). In einer Freiburger Population konnte unter 52 Individuen nur noch ein einziges Tier gefunden werden, das den heimischen mitochondrialen Haplotyp trug. Weitere Populationen im Umkreis, die anfangs als heimische Referenzpopulationen beprobt wurden, zeigten ebenfalls deutliche Muster einer Introgression italienischer Linien (SCHULTE et al. unveröff.).

Generell ist bei solch einer intraspezifischen Hybridisierung zu befürchten, dass regionale Anpassungen (z. B. Eiablagetiefe, Eizeitigung, Phänologie, Physiologie) der heimischen Populationen verschwinden oder zumindest abgeschwächt werden. Hybrid-Populationen können sich auch in ihrer ökologischen Funktion deutlich unterscheiden und ein höheres invasives Potenzial haben (KOLBE et al.2004, KOLBE et al. 2008). Hierdurch sind auch negative Effekte auf andere Arten nicht auszuschließen. Schließlich kann es durch die Kreuzung genetisch entfernt verwandter Linien auch zur »Auszuchtdepression « kommen (z. B. Aufbrechen ko-adaptierter Genkomplexe bis hin zur »Gametenverschwendung« durch Hybridisierung), also zu einem Zusammenbruch der Population durch genetische Inkompatibilitäten (VEITH & SCHMITT 2009).

Zu 2) Eingeschleppte Mauereidechsen stehen im Verdacht, aus bisher wenig bekannten Gründen, heimische Zauneidechsen zu verdrängen (MÜNCH 2001, SCHULTE et al. 2008). Eventuell spielt hierbei das aggressivere Territorialverhalten, die größere Agilität sowie die größere Individuendichte der Mauereidechse eine Rolle. Diese Frage wird zurzeit im Rahmen einer Bachelorarbeit an der Universität Trier untersucht. In 22 Fällen ist die Einschleppung von Mauereidechsen in Lebensräume der

Zauneidechse belegt (Tab. 2). Ein Verschwinden von Zauneidechsen nach dem Einbringen von gebietsfremden Mauereidechsen ist von einigen Standorten dokumentiert (Dortmund, Leipzig: Steinbruch Ammelshain, MÜNCH 2001, SCHULTE 2009).

Zu 3) Im Falle der Ansiedlung von gebietsfremden Mauereidechsen in Gebieten, die nicht von anderen Eidechsen besiedelt sind (z. B. Botanische Gärten), besteht immer die Gefahr einer weiteren Ausbreitung oder erneuten Verschleppung.

Eine heimische Art, zahlreiche gebietsfremde genetische Linien – eine Frage des Bestimmungsmaßstabs?

Nach § 7 Abs. 2 Nr. 8 BNatSchG wird eine wild lebende Tier- oder Pflanzenart als gebietsfremd definiert, »wenn sie in dem betreffenden Gebiet in freier Natur nicht oder seit mehr als 100 Jahren nicht mehr vorkommt«. Da die Mauereidechse natürlicherweise in großen Teilen Deutschlands (mit Ausnahme von Gebieten in Südwestdeutschland und zwei Vorkommen in Südbayern) nicht heimisch ist, muss sie in den übrigen Bereichen als gebietsfremde Art betrachtet werden, solange sie nicht ihr Areal auf natürliche Art und Weise erweitert. Als invasiv wird eine Art nach § 7 Abs. 2 Nr. 9 BNatSchG eingestuft, »deren Vorkommen außerhalb ihres natürlichen Verbreitungsgebietes für die dort natürlich vorkommenden Ökosysteme, Biotope oder Arten ein erhebliches Gefährdungspotential darstellt« (vgl. auch BIDINGER et al. 2011). Demnach werden Arten, die zwar heimisch sind, jedoch aufgrund sich verändernder Umweltbedingungen auch invasiv werden können, in dieser Definition innerhalb ihres natürlichen Areals grundsätzlich als nicht-invasiv eingestuft. Zudem wird in der aktuellen Fassung des BNatSchG eine Art nach § 7 Abs. 2 Nr. 3 als »jede Art, Unterart oder Teilpopulation einer Art oder Unterart« definiert, wobei die wissenschaftliche Bezeichnung für die Einstufung als Art maßgeblich ist. Somit wird dem Einsatz genetischer Methoden und den sich daraus ergebenden wissenschaftlichen Erkenntnissen nicht ausreichend Rechnung getragen, weil auch verschiedene genetische Linien ein erhebliches invasives Potenzial besitzen können.

Zusammenfassend lässt sich festhalten, dass eine Definition der Mauereidechse als invasive Art bislang fehlt, obwohl nach unserer Auffassung klare Belege dafür vorliegen (siehe vorherigen Absatz), die Mauereidechse als solche in die Schwarze Liste invasiver Arten Deutschlands aufzunehmen (ESSL 2008). Ein Grund dafür, dass die zuständigen Naturschutzbehörden oftmals Probleme mit der rechtlichen Auslegung der Aussetzungen haben, ist vermutlich unter anderem im taxonomischen Status invasiver Mauereidechsenlinien zu suchen. Einerseits handelt es sich bei nahezu allen eingeschleppten Tieren um die Art *Podarcis muralis* (Ausnahme: die in Niedersachsen etablierte *Podarcis liolepis*), die als heimische Art und daher als unproblematisch betrachtet wird. Andererseits ist die Erkenntnis über innerartliche Differenzierungen seit der Einführung molekularer Markersysteme deutlich gestiegen. Immer häufiger zeigt sich, dass die traditionellen taxonomischen Eingruppierungen in Art und Unterart nicht haltbar sind. So wurden und werden zahlreiche kryptische Arten ausschließlich aufgrund der Ergebnisse genetischer

Untersuchungen unterschieden und in den Artrang erhoben, obwohl es kaum morphologische Unterscheidungsmerkmale gibt (PINHO et al. 2008, RENOULT et al. 2009, BROOKS & HELGEN 2010).

Die genetischen Linien der Mauereidechse zeigen eine erhebliche Differenzierung und für einige Linien, die auch morphologisch abgrenzbar sind, ist zukünftig zu erwarten, dass daraus taxonomische Konsequenzen gezogen werden. Eine Interpretation dieser Linien als valide Unterarten könnte zu einer anderen Bewertung der Aussetzungen führen. Grundsätzlich wäre aber auch die Aufnahme von genetisch unterschiedlichen Linien in den § 7 Abs. 2 Nr. 3 BNatSchG als Bestimmungsmaßstab einer »Art« bei Vorliegen eines entsprechenden Nachweises sowie eine artspezifische, zeitliche Definition der Generationenanzahl in § 7 Abs. 2 Nr. 7 BNatSchG für die naturschutzfachliche Praxis und den Erhalt der genetischen Vielfalt sinnvoll und richtig.

Handlungsempfehlungen

In Zeiten knapper Mittel für den Naturschutz plädieren wir dafür, nur autochthone Bestände zu schützen und zielgerichtet eine Vernetzung natürlicher Populationen zu verfolgen. Als autochthone Bestände sind in diesem Sinne ausschließlich Vorkommen der Ostfranzösischen Linie (*P. m. brongniardii* im Südwesten Deutschlands) sowie der Südalpen-Linie (*P. m. maculiventris*-West in Südbayern) innerhalb ihres gut dokumentierten natürlichen Areals, nicht aber verschleppte Populationen dieser Linien anzusehen. Ein Schutz allochthoner Populationen, insbesondere an häufig besiedelten Bahnbereichen, könnte zu einer weiteren ungewollten Vernetzung mit autochthonen Vorkommen über Gleisbereiche als Korridore oder zu einer Weiterverschleppung durch den Güterverkehr und schließlich Vermischung mit heimischen Beständen führen. Um diese Möglichkeiten einzugrenzen, sollten allochthone Populationen sowie Hybrid-Populationen keine Schutzmaßnahmen erfahren (ALLENDORF et al. 2001). Es sollte, im Gegenteil, sogar eine Unterlassung von Pflegemaßnahmen (z. B. zur Verhinderung der Sukzession) für diese Vorkommen in Betracht gezogen werden. Ein Abfangen von Individuen ist unserer Meinung nach aufgrund des ungewissen Erfolgs sowie des sehr hohen erforderlichen Aufwands in der Regel nicht sinnvoll. Es wäre hingegen zu überlegen, die nach Eingriffen an allochthonen Mauereidechsen-Populationen gesetzlich erforderlichen Ausgleichsmaßnahmen für heimische Bestände der Art oder auch für Populationen anderer, stärker gefährdeter heimischer Eidechsenarten (*L. agilis*, *L. bilineata*, *L. viridis*, *Z. vivipara*) zu nutzen. Einer entsprechenden Erweiterung des Katalogs von Ausgleichsmaßnahmen im Falle unvermeidlicher Eingriffe stehen unserer Meinung nach keine naturschutzfachlichen Bedenken entgegen.

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SUMMARY

Increasing human population, international commerce and mobility are accelerating the introduction of biota to a formerly unknown extent. Consequently, intended and unintended introductions of non-native species are recognized as a severe problem in nature conservation. The Common wall lizard (*Podarcis muralis*), a species with a sub-Mediterranean native distribution, has established more than 150 non-native populations in Central Europe. This species represents an ideal model system to examine the role of the source region on establishment success, to assess the genetic consequences of biological invasions, and to study the consequences of intraspecific hybridization on native wall lizard lineages. I performed a 'top-down approach', aiming to identify the prerequisites first, and subsequently narrowing the perspective towards potential causal mechanisms and evolutionary processes.

The adaptive capabilities and wide distribution of many species implicate that the quality and breadth of ecological niches vary across time, space and therefore among populations and evolutionary lineages. To test this hypothesis, I analysed for the first time whether climatic niches differ at the intraspecific level in invasive species (**Chapter I**). I assigned 77 introduced populations in Central Europe to eight geographically distinct evolutionary lineages using DNA barcoding. The resulting dataset was used in combination with species distribution models (SDMs) based on climatic information from native and invasive ranges to test for intraspecific niche divergence. The analysed lineages had rather similar realised niches in their native and invasive ranges, whereas inter-lineage niche differentiation was comparatively strong. However, I found only a weak correlation between geographic origin (i.e. mtDNA-lineage) and invasive occurrence. Lineages with narrow realised niches still became successful invaders far outside their native range, most probably due to broader fundamental niches. The results indicate that the observed niche differentiation among evolutionary lineages is mainly driven by niche realisation and not by differences in the fundamental niches. Furthermore, the findings suggest that cryptic niche conservatism may in general explain the invasion success of species in areas with apparently unsuitable climate.

The wide applicability of genetic tools in conservation biology requires the development of minimal-invasive or non-invasive DNA sampling techniques. To adequately address questions of population genetics in this thesis ca. 800 individuals had to be genotyped. Since tail-clipping harms the locomotory performance and energy reserves of wall lizards, I compared the quantity and quality of the isolated DNA collected from buccal swabs and tail tips in **Chapter II**. These results show that buccal swabs are a simple and efficient non-invasive sampling method for DNA analysis in adult lacertid lizards.

In **Chapter III**, I determined the geographic origin of the northernmost introduced population of the Italian wall lizard *Podarcis siculus* in Rapperswill, Switzerland. This population originated from a region between the Po plain (Italy) and the northern Adriatic region (Croatia). **Chapter IV** comprises the first record of *P. liolepis* introduced in Germany within a syntopic population of its congener *P. muralis*. The founder individuals presumably stem from a region in the eastern Pyrenees, where sympatric populations are known. In concordance with behavioural observations, no evidence for gene flow between the two species was found. Compared to the analysed native populations, high levels of genetic diversity have been retained in the introduced population of both species.

Chapter V provides the first evidence for intraspecific hybridisation between native and introduced wall lizard lineages along the Upper Rhine Rift. As a devastating consequence of introductions, a rapid genetic assimilation of native wall lizard populations caused by strong introgression from introduced Italian lineages could be demonstrated. The genetic diversity of hybrid populations was substantially higher than in introduced and native populations belonging to a single lineage but, in contrast to previous studies, the relationship between genetic diversity and admixture level was non-linear and rapidly reached a plateau of high genetic diversity at an admixture level of two. However, even introduced populations with low founder sizes and from one source population retained moderate levels of genetic diversity and no evidence for a genetic bottleneck was found. The extent of introgression and the dominance of alien haplotypes in mixed populations indicate that introductions of non-native lineages represent a significant threat for the genetic integrity of native populations due to the rapid creation of hybrid swarms.

Fine scale genetic analyses of evolutionary processes acting at the invasion front of expanding populations have rarely been performed at a local scale. I analysed spatial patterns of genetic variation within an expanding introduced wall lizard population in Passau (**Chapter VI**). The results demonstrate that significant genetic population structure can emerge rapidly at a small spatial scale. The genetic differentiation tended to increase, while the genetic diversity declined from the centre of introduction towards the expanding range margin. I assume that the pronounced territoriality of *P. muralis*, which results in 'high rates' of noncontiguous and stratified dispersal from longer established sites, is sufficient to maintain genetic diversity despite founder events at the invasion front.

The final **Chapter VII** summarises most of the important findings of this thesis in order to provide information for field herpetologists and conservationists. Furthermore, I address the difficult phenotypic assignment of populations to evolutionary lineages and discuss the problem of how to deal with invasive populations in the light of the current conservation legislation.

ZUSAMMENFASSUNG

Der Anstieg der Weltbevölkerung, des internationalen Warenhandels und der Mobilität fördert die Einschleppung von Biota in bislang ungeahntem Ausmaß. Infolgedessen werden beabsichtigte und unbeabsichtigte Einschleppungen gebietsfremder Arten als zunehmend großes Problem im Naturschutz betrachtet. In Mitteleuropa haben sich mehr als 150 gebietsfremde Populationen der ursprünglich submediterran verbreiteten Mauereidechse (*Podarcis muralis*) etabliert. Diese Art verkörpert ein ideales Modellsystem zur Untersuchung der Rolle des geografischen Ursprungs für den Etablierungserfolg, zur Überprüfung genetischer Konsequenzen von biologischen Invasionen sowie zur Untersuchung der Auswirkungen intraspezifischer Hybridisierung auf heimische Mauereidechsen-Linien. Über eine anfängliche Identifikation von Voraussetzungen zur Etablierung wurden darauffolgend potentiell ursächliche Mechanismen und evolutionäre Prozesse untersucht.

Die Anpassungsfähigkeit und Verbreitungsmuster zahlreicher Arten implizieren, dass die Qualität und Breite von ökologischen Nischen über Zeit und Raum und damit auch zwischen Populationen und evolutionären genetischen Linien variiert. Um diese Hypothese zu überprüfen, wurde in **Kapitel I** erstmals getestet, ob sich die Klimanische einer invasiven Art intraspezifisch unterscheidet. Über eine DNA-Sequenzierung wurden 77 eingeschleppte Populationen in Zentral Europa acht unterschiedlichen geografisch klar abgrenzbaren evolutionären Linien zugeordnet. Der gewonnene Datensatz wurde in Kombination mit auf klimatischen Informationen des nativen und invasiven Areals basierenden Artverbreitungsmodellen (SDMs) zur Überprüfung intraspezifischer Nischendivergenz genutzt. Die Linien zeigten jeweils ähnliche realisierte Nischen in ihren ursprünglichen und invasiven Arealen, wohingegen die Nischendifferenzierung zwischen den Linien vergleichsweise stark war. Die Korrelation zwischen geographischem Ursprung (mtDNA-Linie) und invasivem Vorkommen war schwach und es kann vermutet werden, dass Linien mit enger realisierter Nische aufgrund ihrer breiten fundamentalen Nische dennoch in der Lage sind erfolgreich Gebiete weit außerhalb ihres ursprünglichen Areals zu kolonisieren. Die beobachtete Nischendifferenzierung zwischen den Linien beruht vermutlich hauptsächlich auf der Realisierung ihrer Nische, nicht aber auf Unterschieden in der fundamentalen Nische. Die Ergebnisse implizieren, dass kryptischer Nischenkonservatismus den Invasionserfolg von Arten in Gebieten mit scheinbar ungeeignetem Klima häufiger erklären könnte.

Die weite Anwendung genetischer Methoden in der Naturschutzbiologie verlangt die Entwicklung minimal-invasiver oder nicht-invasiver Methoden zur DNA Gewinnung. Da für die populationsgenetischen Fragestellungen dieser Arbeit etwa 800 Individuen genotypisiert wurden und die Entnahme von Schwanzspitzen zu einer Einschränkung der Bewegungsfähigkeit und zu einem Verlust an Fettreserven bei Eidechsen führt, wurde eine alternative Beprobungsmethode getestet. Dazu wurde die Menge und Qualität an isolierter DNA verglichen, die durch Mundschleimhautproben und durch Gewebeproben gewonnen wurde (**Kapitel II)**. Die Ergebnisse zeigen, dass Mundschleimhautproben eine einfache und effiziente nicht-invasive Beprobungsmethode für DNA-Analysen bei adulten Lacertiden darstellen.

In **Kapitel III**, wurde der geographische Ursprung der nördlichsten eingeschleppten Ruineneidechsen-Population (*Podarcis siculus*) in Rapperswill, Schweiz bestimmt. Die Gründerindividuen der Population stammen aus einer Region zwischen der Poebene (Italien) und der nördlichen Adria (Kroatien).

Kapitel IV beinhaltet den ersten Nachweis einer Einschleppung der Katalonischen Mauereidechse (*P. liolepis*) innerhalb einer syntopen *P. muralis* Population in Deutschland. Die Gründerindividuen stammen vermutlich aus einer Region in den östlichen Pyrenäen, aus der sympatrische Vorkommen dokumentiert sind. In Übereinstimmung mit Verhaltensbeobachtungen wurde kein Hinweis auf Genfluss zwischen beiden Arten gefunden. Im Vergleich zu natürlichen Populationen erhielt sich innerhalb beider eingeschleppter Populationen eine hohe genetische Diversität.

Kapitel V deckt erstmals intraspezifische Hybridisierungen zwischen heimischen und eingeschleppten Mauereidechsen-Linien entlang des Oberrheingrabens auf. Als eine verheerende Auswirkung von Einschleppungen konnte eine schnelle und gründliche genetische Assimilation natürlicher Mauereidechsen-Populationen durch eine starke Introgression eingeschleppter italienischer Linien nachgewiesen werden. Die genetische Diversität der Hybridpopulationen war um ein Vielfaches höher als die innerhalb eingeschleppter oder natürlicher Populationen, die auf eine genetische Linie zurückgehen. Im Gegensatz zu bisherigen Studien war der Zusammenhang zwischen genetischer Diversität und Durchmischungsgrad jedoch nicht-linear und erreichte frühzeitig ein Plateau hoher genetischer Diversität bei einer Vermischung von zwei Linien. Nichtsdestotrotz bewahrten auch eingeschleppte auf wenige Gründerindividuen einer Ursprungspopulation zurückgehende Vorkommen eine moderate genetische Diversität und wiesen keine Anzeichen eines genetischen Flaschenhalses auf. Das Ausmaß an Introgression und die Dominanz gebietsfremder Haplotypen innerhalb gemischter Populationen zeigt, dass Einschleppungen die genetische Integrität natürlicher Populationen durch die schnelle Bildung von Hybridschwärmen stark gefährden.

Kleinräumige genetische Analysen von evolutionären Prozessen, die am Expansionsrand von Populationen stattfinden, wurden nur selten auf lokaler Ebene durchgeführt. In **Kapitel VI** wurde die räumliche Verteilung der genetischen Variation innerhalb einer expandierenden eingeschleppten Mauereidechsen-Population in Passau analysiert. Die Ergebnisse zeigen, dass eine signifikante genetische Strukturierung innerhalb einer Population sehr schnell und kleinräumig entstehen kann. Außerdem zeigen die Ergebnisse die Tendenz eines Anstiegs an genetischer Differenzierung bei gleichzeitiger Abnahme der genetischen Diversität vom vermuteten ursprünglichen Aussetzungsort hin zum Expansionsrand. Ich vermute, dass die ausgeprägte Territorialität von *P. muralis*, die sich in einer häufigen Ausbreitung über große Distanzen und von etablierten Standorten aus zeigt, ausreicht, um die genetische Diversität trotz starker Gründereffekte an der Invasionsfront aufrecht zu erhalten.

Das abschließende **Kapitel VII** fasst die wichtigsten Resultate dieser Arbeit mit dem Ziel zusammen, die Informationen dem Naturschutz zugänglich zu machen. Darüber hinaus wird die schwierige phänotypische Zuordnung von Populationen zu evolutionären Linien sowie das Problem des naturschutzrechtlichen Umgangs mit Einschleppungen diskutiert.