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ORIGINAL PAPER

# Strong genetic differentiation due to multiple founder events during a recent range expansion of an introduced wall lizard population

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**Abstract** Biological invasions represent ideal systems for the study of evolutionary processes associated with colonization events. It has been hypothesized that the genetic diversity is generally decreasing from the centre of the range to the margins due to multiple founder events. Invasive populations offer the opportunity to test this hypothesis at a fine spatial and temporal scale. We analysed the genetic structure of a large expanding non-native population of the Common Wall Lizard (*Podarcis muralis*) in Passau (Germany) using thirteen microsatellite loci. We analyzed the genetic structure and levels of admixture across a transect reflecting the expansion process and tested for a loss of genetic diversity and an increase of genetic differentiation from the centre to the invasion front. Our results demonstrate that significant genetic population structure can emerge rapidly at a small spatial scale. We found a trend for an increase in genetic differentiation and a decrease in genetic diversity from the invasion centre to the expanding range margin, suggesting that genetic drift is the major factor causing this pattern. The correlation between genetic diversity and average genetic differentiation was significant among sites. We hypothesize that the territoriality of *P. muralis* generates sufficient rates of noncontiguous and stratified dispersal from longer established sites to maintain significant genetic diversity at the invasion front. Simultaneously, territoriality might restrict the colonization success of migrants at established sites, so that in combination with founder events a strong differentiation arises.

**Keywords** Dispersal · Founder event · Genetic differentiation · Invasive species · Microsatellite · Range expansion

## Introduction

The increasing 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 focused on 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 and 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

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into the intrinsic factors that determine invasion success (Ramakrishnan et al. 2000). The genetic processes associated with biological invasions are likely to be rather similar to those found during natural range expansions (Hampe and Petit 2005). However, most genetic studies on invasive species either focus on the differentiation of invasive populations from their ancestral source population (Bossdorf et al. 2005; Lockwood et al. 2007) or investigate genetic structure at a large geographic scale (e.g. Eckert et al. 2008). Only a few studies address the interplay between range expansion and genetic variation at small spatial and temporal scales within founding populations (Herborg et al. 2007; Dlugosch and Parker 2008; Parisod and Bonvin 2008; Björklund and Almqvist 2010; Short and 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; Hampe and Petit 2005; Eckert et al. 2008). Genetic diversity is thought to decrease due to recurrent founder effects, small effective population sizes, partial isolation and strong 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 lead to sharp allele frequency gradients, which might be the key drivers for genetic differentiation in nascent colonizing populations at the expansion front (Excoffier and Ray 2008). Moreover, it has been shown that potential 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 and Parker 2008). Indeed, recent studies have documented recombination of different source genotypes (Dlugosch and Hays 2008), surfing of low-frequency alleles at the front of expansion (Excoffier and Ray 2008) or 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 and Bonvin 2008).

The spatiotemporal distribution of genetic variability 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 little information available on dispersal modes and their contribution to fluctuations in effective population sizes at the edge of range expansions (Estoup et al. 2004; Ramakrishnan et al. 2000). 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, such as the island model of migration (Wright 1942), stepping-stone model (Kimura and Weiss 1964) or isolation by distance (Wright 1942). While diffusion is leading to a gradual spread over a period of generations (classic isolation by distance pattern), long-distance dispersal is thought to result in the establishment of pioneer clusters far away from their source, often exhibiting severe genetic bottlenecks (Petit et al. 1997; Wilson et al. 2009). Interestingly, a recent study indicates that dispersal modes can change along time (Ramakrishnan et al. 2000). 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 (so called "stratified dispersal"; Shigesada et al. 1995). In addition to intrinsic (e.g. behavioural and life history traits) and extrinsic factors (e.g. landscape patterns) which influence dispersal mode and rate, human assisted jump-dispersal 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). This might be particularly true for urban areas, where anthropogenic influences are particularly strong.

Thriving invasive populations provide ideal conditions to study spatial and temporal patterns of genetic variation during colonization events. Recent fine scale genetic analyses of range expansions provided first evidence that significant genetic structure can arise at very small spatial and temporal scales (Short and Petren 2011). In this study, we assess spatial patterns of genetic structure and genetic diversity within a non-native expanding population of the Common Wall Lizard (*Podarcis muralis*) in south-eastern Germany. *P. muralis* is a synanthropic lacertid lizard with a sub-Mediterranean native distribution, which has successfully colonized part of 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 well documented (Schulte et al. 2011b, 2012a). Based upon the unique combination of morphology (Tuscany Clade colour pattern) and mtDNA haplotype (Venetian Clade), the source area of this population has been assigned to a relatively small area in Italy (Bologna-Modena region), where natural hybrids between both lineages occur (W. Mayer & S. Schweiger pers. comm.). The founder individuals have presumably been introduced during the 1930s (Lentner 1936) or 1940s (personal comm. of residents). The species has meanwhile colonized a range of about 25 km (Schulte 2008). We performed a microsatellite analysis (1) to examine the genetic structure across a transect covering nearly the entire colonized range and reflecting the colonization history, and (2) to test the hypothesis of 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). In order to cover the routes of expansion across the complete colonized range, we sampled individuals at five sites along an 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 documenting their spread since the introduction. Based upon this information, it is inferred that the species has colonized HA in the 1960s and PA after establishment at VE in the 1930s or 1940s. OB has to be considered as the most recently colonized site (before 1975, Assmann, unpublished data, Fröer, unpublished data) close to the edge of the expansion at neighboring sites at the Austrian border. Since the mid s the abandoned Danube railway track from Passau to Obernzell has been colonized (Assmann, unpulished data), afterwards the species has spread into urban areas and tributary valleys. DNA samples were collected by buccal swabbing each specimen using a diagnostic fine-tip dry swab (Medical Wire and Equipment, MW-100) (for details see Schulte et al. 2011a). Samples were stored in sterile tubes at −20 °C; DNA was extracted using the Qiagen DNEasy blood and tissue kit following the manufacturer's protocol (adding PBS buffer).

### Assignment of geographic origin

In a former study (Schulte et al. 2008), we sequenced an 887 base pair (bp) fragment of the mitochondrial cytochrome *b* gene (cyt *b*) using the primers Sicnt (5′-TTTGGATCCCTGTTAGGCCTCTGTT-3′) and Melcb-H (3′-ATAATAAAAGGGGTGTTCTACTG GTTGGCC-5′) of two individuals from Obernzell (OB) (Genbank accession numbers: HQ652923, HQ652924). We now sequenced two individuals from Passau-Grubweg (PA) and one individual from Veste Oberhaus (VE) to obtain a better coverage of the invasive range in Passau. Sequencing was performed with the DYEnamic ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich) for sequencing reactions run on a MegaBACE 1,000 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. For lineage identification see Schulte et al. (2012a, 2012b). Additionally we documented the dorsal and ventral colour pattern of all individuals, which is specific for Central Italian lineages (e.g. Tuscany and Venetian Clade).

### Genotyping

We genotyped all individuals at thirteen microsatellite loci, which have been developed for *P. muralis* (A7, B3, B4, B6, B7, C8, C9; Nembrini and Opplinger 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

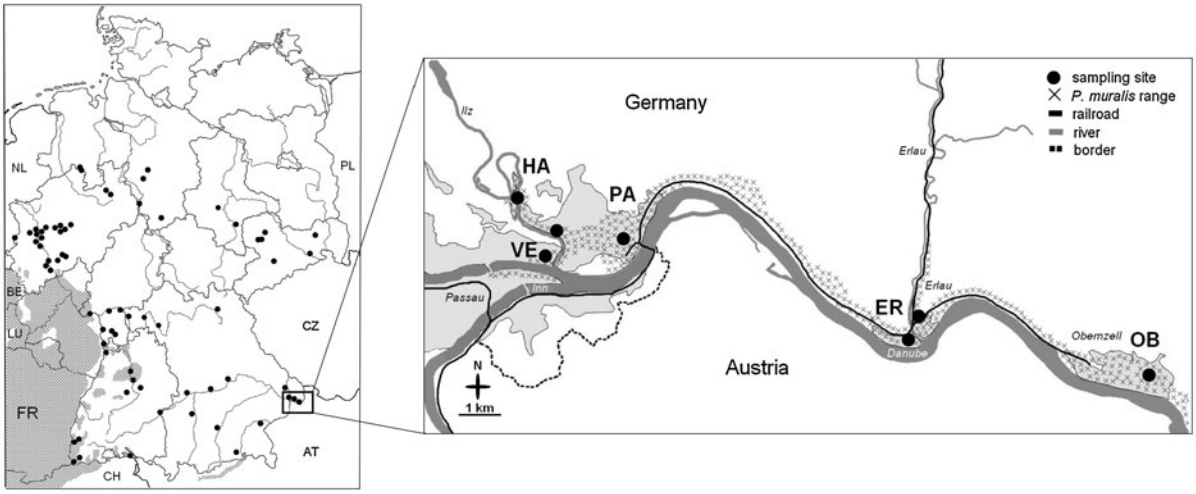

**Fig. 1** Native (*shaded area*) and invasive (*black dots*) distribution of *P. muralis* (Schulte 2008) and location of the study site in Germany as well as location of sampling sites across the colonized range of the species in the Passau region in Germany (*HA* Hals (Ruine), *VE* Veste Oberhaus, *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)

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: 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: 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 1,000 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 2001). STRUCTURE 2.3.3 (Pritchard et al. 2000) was used to detect genetic structure across the sampled range. 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 genetic cluster was obtained by STRUCTURE to separate admixed from purebred individuals (Vähä and Primmer 2006). We chose a conservative threshold value of $Q = 0.20$–$0.80$ to detect 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 and vonHolt 2011) to analyse the results.

GenAlEx 6.5 (updated from Peakall and Smouse 2012) was used 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), particularly in the context of invasions, where non-equilibrium situations are likely to occur (Fitzpatrick et al. 2012), it has been shown to be still useful (Ryman and Leimar 2009; Meirmans and Hedrick 2011). We calculated $F_{ST}$ in an AMOVA with 9,999 iterations in GenAlEx using the genetic clusters suggested by STRUCTURE (Ryman and Leimar 2009). Additionally, we calculated $D_{est}$ values in GenAlEx.

We tested for a correlation between genetic diversity ($A_R$) as well as 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. 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 1,000 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 $N_e$ (2–5,000). After executing five iterations of estimating $N_e$ we calculated the mean and standard deviation of $N_e$ for all sites pooled.

## Results

### Geographic origin, population structure and genetic differentiation

The analysed individuals from Veste Oberhaus (VE), Passau-Grubweg (PA) and Obernzell (OB) all carried an identical mtDNA haplotype matching native haplotypes of the Venetian Clade, Italy (DQ001032, Podnar et al. 2007). The unique combination of the Venetian Clade haplotype and morphological characteristics (green back, black dotted belly) of the Tuscany Clade suggests that the founder individuals stem from the narrow contact zone of these two lineages in the Bologna-Modena region (Fig. 2).

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 <0.2, all loci were kept for further analyses. There was no evidence for large allele dropout 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 $K = 5$ (Fig. 3).

**Fig. 2** Presumed location of the source population in Italy as well as the native range of the Tuscany and Venetian Clade (*diagonal shaded areas*) and their hybrid zone

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 $F_{ST}$ and $D_{est}$ values were significant (Table 1) and both values correlated significantly with each other (linear regression, $R^2 = 0.97$, $P < 0.001$). $F_{ST}$ 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. 4b). However, no significant isolation-by-distance was found (Mantel test, $R^2 = 0.0458$, $P = 0.305$, $N = 10$ pair-wise comparisons).

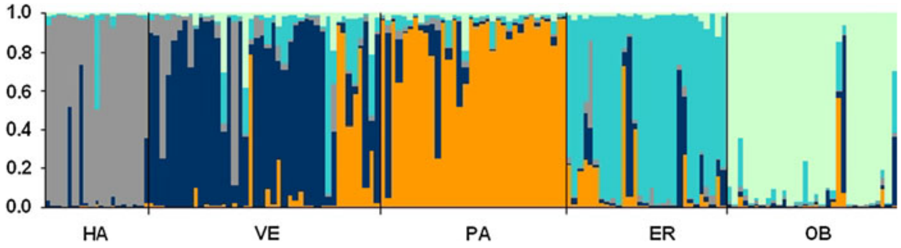

**Fig. 3** Genetic clusters obtained from the STRUCTURE analysis ($K = 5$) for all 155 samples. Each individual is represented by a single vertical line, divided into $K$ colours. The coloured segment shows the individual's estimated proportion of membership to that genetic cluster. *HA* Ruine Hals, *VE* Veste Oberhaus, *PA* Passau Grubweg, *ER* Erlautal, *OB* Obernzell

**Table 1** Pairwise $F_{ST}$ values (lower left part) and $D_{est}$ values (upper right part) among sampling sites

| | HA | VE | PA | ER | OB |
|---|---|---|---|---|---|
| **HA** | | 0.235 | 0.407 | 0.236 | 0.394 |
| **VE** | 0.069 | | 0.139 | 0.138 | 0.191 |
| **PA** | 0.129 | 0.042 | | 0.200 | 0.217 |
| **ER** | 0.074 | 0.038 | 0.062 | | 0.276 |
| **OB** | 0.138 | 0.062 | 0.079 | 0.093 | |

All pairwise $F_{ST}$ and $D_{est}$ values were significant

Samples from three of the five sites were composed of genetically rather homogeneous clusters, whereas at two sites several genetic clusters were found (VE and ER; Figs. 3, 4c). 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 showed large proportions (40.5 %, see Fig. 4c) 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 site (PA) maintained the most homogeneous genetic cluster with 79.7 % ($N = 27$) of all individuals belonging to it, 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 showed similar large proportions of mixed ancestry (37.9 %) as VE, while 55.2 % ($N = 16$) of all individuals from this site belonged to the most common cluster (ER) (Fig. 4c). Gene flow was suggested between ER and VE and PA, but lacking with site OB. The last cluster (OB) represented a rather homogeneous cluster (83.9 % belonging to 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 (Table 2). Sites at the range margin (HA and OB) had the lowest allelic richness, whereas VE, the centre of introduction, retained the highest allelic richness (6.30, Fig. 4a). 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 ($F_{IS} = 0.03$). The estimated $N_e$ of the entire population (all sites combined) was 840 ± 3.69.

## Discussion

Our results show that genetic population structure arose rapidly during the invasion of wall lizards at a small spatial scale. This result was surprising when considering the small geographic distances between sites (mean 9.7 km), the high mobility of the species (Schulte 2008) and the existence of suitable dispersal corridors (railway tracks) within a continuous range. However, our results are in line with recent findings from range expansions of other invasive species (Dlugosch and Parker 2008; Ramakrishnan et al.

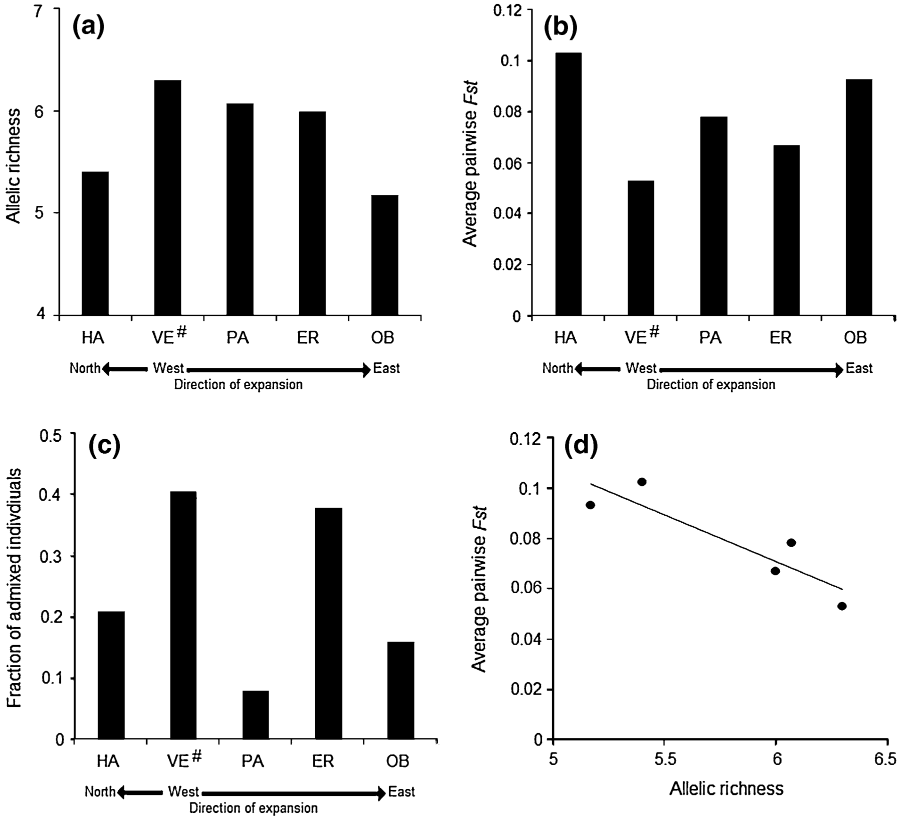

**Fig. 4** Relationship between direction of expansion ($VE^{\#}$ = presumed introduction site) and **a** allelic richness, **b** genetic differentiation, **c** the fraction of admixed individuals at sites and **d** correlation of genetic diversity and genetic differentiation

**Table 2** Comparison of genetic variability among sites

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

$N$ = number of samples, $N_A$ = mean number of alleles, $A_R$ = allelic richness (corrected for the minimum sample size of 19 individuals), $H_O$ and $H_E$ = observed and expected heterozygosities, $F_{IS}$ = inbreeding coefficient

2000; Short and Petren 2011). The geographic patterns of genetic variation strongly matches the expected patterns found in natural ranges of species (Eckert et al. 2008; Hampe and Petit 2005), which have also been found in the native range of the wall lizard (Gassert et al. 2013). Although not significant, we also found a slight decrease of genetic diversity from the centre to the invasion front. 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). However, this association can be expected as random genetic drift will lead to the loss of different alleles in different populations, which decreases the overlap in allele frequencies and thus leads to increased differentiation.

## Rapid genetic differentiation

The reasons for the strong genetic structure 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 and 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 and Petren 2011) as well as in a North American wall lizard population (Cincinnati) stemming from a single founder event (Lescano 2010). Another explanation for this pattern, which can not be ruled out might be human-mediated secondary translocations of individuals from established sites in Passau to nearby locations.

In addition to founder effects, the invader's behaviour during the invasion process may also affect the resulting genetic population structure (Holway and Suarez 1999). Kin-based colonization with high levels of relatedness at sites producing a large number of colonizers has been shown for the common lizard *Z. 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 defend their home ranges and monopolize 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 of migrants at colonized sites, so that population differentiation will further increase. Within isolated and dense non-native populations of the wall lizard (e.g. Ammelshain, Steinicke, unpulished data; Cincinnatti, Brown et al. 1995) a decrease of home range size has been 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 connecting 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

Based upon the historical records, the mean speed of the range expansion from West to East was ca. 500 m/year. Similar expansion rates per year (440 m/year) have been suggested for an introduced population in Liechtenstein (Kühnis and Schmocker 2008) and in the introduced population in Cincinnati (350 m/year; Hedeen and Hedeen 1999). Movement distances of *P. muralis* inferred from mark-recapture studies range from 50 m/h to 500 m/1–3 years (Schulte 2008). However, maximum movement distances of up to 1,000 m/day have been documented for juveniles, suggesting a stronger dispersal ability of this cohort (Stumpel 2004). Furthermore, it is likely that mark-recapture analyses underestimate the species' dispersal ability since 40–60 % of the lizards marked in these studies have never been recaptured (Boag 1973; Dexel 1986; Brown et al. 1995). It is reasonable 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 and Hedeen 1999; Kühnis and 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 Passau population has a high genetic diversity comparable to mixed populations stemming from several source regions rather than to other purebred introduced or native wall lizard populations in Central Europe (Altherr 2007; Schulte et al. 2012c). This may be due to the source region of the founders, 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 and Aronson 2010; Giovannotti et al. 2010; Bellati et al. 2011; Gassert et al. 2013). It is also likely that propagule pressure during introduction was rather high. 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 in intended introductions of reptiles.

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 and Petit 2005) and has been also found in other fine scale genetic analyses of range expansions (Short and Petren 2011). The decline of genetic diversity follows the direction of expansion and is most likely the result of founder events (Hochkirch and Damerau 2009). In contrast, continuous gene flow among adjacent populations might have generated the higher genetic diversity close to the introduction site. These patterns also support the assumption of a single introduction of founder individuals in VE, as it seems unlikely that someone collected individuals twice from the same (small) region in Italy (which does not belong to a major touristic region) and that such a second introduction led to a smaller genetic diversity at the invasive range margin. The estimated effective population size in the Passau population (840 individuals) is very high and exceeds effective population sizes of 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 high habitat suitability, including the existence of various dispersal corridors and missing competition.

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