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Plastic and genomic change of a newly established lizard population following a founder event

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Abstract

Understanding how phenotypic divergence arises among natural populations remains one of the major goals in evolutionary biology. As part of competitive exclusion experiment conducted in 1971, 10 individuals of Italian wall lizard (*Podarcis siculus* (Rafinesque-Schmaltz, 1810)) were transplanted from Pod Kopište Island to the nearby island of Pod Mrčaru (Adriatic Sea). Merely 35 years after the introduction, the newly established population on Pod Mrčaru Island had shifted their diet from predominantly insectivorous towards omnivorous and changed significantly in a range of morphological, behavioural, physiological and ecological characteristics. Here, we combine genomic and quantitative genetic approaches to determine the relative roles of genetic adaptation and phenotypic plasticity in driving this rapid phenotypic shift. Our results show genome-wide genetic differentiation between ancestral and transplanted population, with weak genetic erosion on Pod Mrčaru Island. Adaptive processes following the founder event are indicated by highly differentiated genomic loci associating with ecologically relevant phenotypic traits, and/or having a putatively adaptive role across multiple lizard populations. Diverged traits related to head size and shape or bite force showed moderate heritability in a crossing experiment, but between-population differences in these traits did not persist in a common garden environment. Our results confirm the existence of sufficient additive genetic variance

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for traits to evolve under selection while also demonstrating that phenotypic plasticity and/or genotype by environment interactions are the main drivers of population differentiation at this early evolutionary stage.

KEYWORDS
bottleneck, heritability, invasive success, phenotypic plasticity, population crossing experiment, rapid evolution

1 | INTRODUCTION

One of the fundamental questions in evolutionary biology is how natural selection contributes to phenotypic variability in natural populations. However, the pattern and strength of selection is dictated by temporal and spatial ecological variation, which directly affects our ability to observe adaptive processes in nature. The polygenic nature of complex phenotypic traits further hampers the detection of adaptation footprints, especially across populations inhabiting environments characterized by mild selection pressures (Pritchard & Di Rienzo, 2010). When environmental conditions abruptly change or a population occupies a novel habitat, selection may increase the genome-wide abundance of favoured alleles and create adaptive genomic divergence (Endler, 1986; Nosil et al., 2009). Such shifts can result in rapid evolution of phenotypically and genetically distinct populations over the course of only several generations (Carroll et al., 2007; Marques et al., 2018; Stuart et al., 2014). Adaptive evolution occurs through genetic changes but is often preceded by an adaptive plasticity, which increases phenotypic adaptive values (Ghalambor et al., 2007). Though plasticity appears to be most advantageous in fluctuating environments, plastic responses may also play a relevant role in species colonization and persistence in novel habitats (Aubret & Shine, 2009; Lande, 2015; Wang & Althoff, 2019). Eco-evolutionary studies focusing on phenotypic divergence in natural populations have been hard-pressed to determine the relative contributions of phenotypic plasticity and genomic divergence to adaptation across spatial and temporal scales (Hendry, 2013). Phenotypic plasticity and adaptive evolution frequently co-occur, with plasticity either constraining or facilitating genomic adaptation (Lande, 2009; Oostra et al., 2018). Both theory and empirical data suggest that initial plastic modifications attuned to adaptive demands can promote subsequent genetic adaptation to new habitats (Levis et al., 2018; Noble et al., 2019; Radersma et al., 2020). Although the role of plasticity in adaptive trajectories cannot be denied, adaptive evolution only occurs through transmission of genetic responses to selective pressures across generations. Therefore, it is the extent of the variability of the trait that can be transmitted to the next generation (i.e. its heritability) that governs the rate and magnitude of trait evolution (De Villemereuil et al., 2015; Falconer & Mackay, 1996). Narrow-sense heritability (h^2) is the proportion of total phenotypic variation that is due to additive genetic variance (V_A) among individuals. It is of special concern for adaptive evolution, as it determines the responsiveness of a trait to selection and offers a useful measure of adaptive potential of a phenotypic trait in a population (Allendorf et al., 2013; Hoffmann et al., 2017). Accordingly, estimating heritability provides a good opportunity to evaluate the relative role of genetic and plastic mechanisms underlying that trait in a specific population.

Detecting evolution by natural selection in the wild thus requires demonstrating that the phenotypic trait is variable, and adaptive (i.e. improve fitness for individuals), that the observed variability has a genetic basis (i.e. is heritable), and that it promotes genomic divergence in trait-associated loci (irrespective of any neutral sources of variation) (Endler, 1986; Pardo-Diaz et al., 2015). This can be notably difficult to achieve, as it calls for an extensive application of various experimental approaches, quantitative genetics modelling and modern population genomics techniques (Gienapp et al., 2017; Pardo-Diaz et al., 2015; Schlötterer et al., 2015). However, those are also the first steps in inferring the evolutionary potential of contemporary populations and predicting their response to subsequent ecological change.

The importance of genetic variance for population fitness has been postulated a long time ago (Nei et al., 1975). Reductions of genomic variation in natural populations are often the consequence of bottlenecks, which occur due to sharp reductions in effective population size following severe ecological disturbance. Founder effect refers to specific bottleneck event attributable to a small number of individuals establishing a novel population (Mayr & Provine, 1980). Irrespectively of their ecological cause, bottlenecks commonly increase the genetic drift and inbreeding. The size of a founding population is hence known to be one of the most important factors driving its future evolutionary trajectory in a novel environment (Allendorf, 1986) because it directly influences available phenotypic and genetic variance. Yet, many aspects of the bottleneck's determining power for colonization success and/or subsequent adaptation to novel environments still remain unresolved, especially in regard to the amount of additive genetic variance retained, or the interacting effects of phenotypic plasticity or gene flow (Dlugosch & Parker, 2008; Estoup et al., 2016; Radersma et al., 2020; Roman & Darling, 2007).

Biological invasions oftentimes represent a good model system to study the basis of adaptive responses in natural ecosystems. They are frequently well documented, enabling precise measurement of the speed of phenotypic trait evolution, and can trigger remarkable phenotypic shifts in introduced and native populations alike (Cattau et al., 2018; Moran & Alexander, 2014; Stuart et al., 2014).

Evolutionary consequences of biological invasions are recurrently studied on islands (Feiner et al., 2021; Kolbe et al., 2004; Sendell-Price et al., 2021; Warren et al., 2015), as their geographical isolation and often contrasting ecological conditions enable more accurate characterization of crucial ecological and demographic parameters. Ever since Darwin, island systems have remained one of the most fascinating scientific arenas for studying how populations and species diverge. One recent intriguing example of rapid phenotypic evolution comes from the deliberate introduction of the Italian wall lizard (*Podarcis siculus* (Rafinesque-Schmaltz, 1810)) on a small islet of Pod Mrčaru in the Adriatic Sea off the cost of Croatia. In a transplant experiment conducted in 1971, five pairs of *P. siculus* from the islet of Pod Kopište were introduced on the nearby islet Pod Mrčaru (Figure 1; Figures S1 and S2), which was at the time inhabited by Dalmatian wall lizard, *Podarcis melisellensis* (Gorman et al., 1972). Follow-up studies have revealed that in only 35 years *P. siculus* completely outcompeted the native *P. melisellensis* on the islet (Herrel et al., 2008; Vervust et al., 2007). This was not entirely unexpected, as *P. siculus* is considered an invasive species across its introduced range, known to often displace native lizard populations by reducing or taking over their habitat (D'Amico et al., 2018; Putman et al., 2020). Nevertheless, the surveys exposed something more interesting – in this short period of time the newly established *P. siculus* population exhibited spectacular phenotypic changes in ecology, morphology and physiology (Herrel et al., 2008; Taverne et al., 2019; Vervust et al., 2010; Wehrle et al., 2020). Many of the observed morphological and functional changes, such as difference in bite force, head size and shape, are reminiscent of the adaptations found in herbivorous species (Herrel, 2007; Herrel et al., 2004) and can be connected to the observed ecological shift from a predominantly insectivorous to an omnivorous diet. The adaptive role of variation in cranial shape and jaw muscles of *Podarcis* lizards is evident by consistency of ecological conditioning of their form and function across evolutionary scales, from populations to species (Taverne et al., 2021). Phenotypic head traits related to higher bite force in Italian wall lizards allow them access to a wider range of trophic resources (Taverne et al., 2020). Even though the amount of plant consumed is the major predictive ecological covariate of the head shape, sexual competition and prey hardness also affect head morphology (Taverne et al., 2020, 2021, 2023). The relative role of phenotypic plasticity and genomic adaptation in the observed differentiation, however, remained unknown, as did the signatures of small founder size and the subsequent phenotypic shift on genomic patterns in the introduced population.

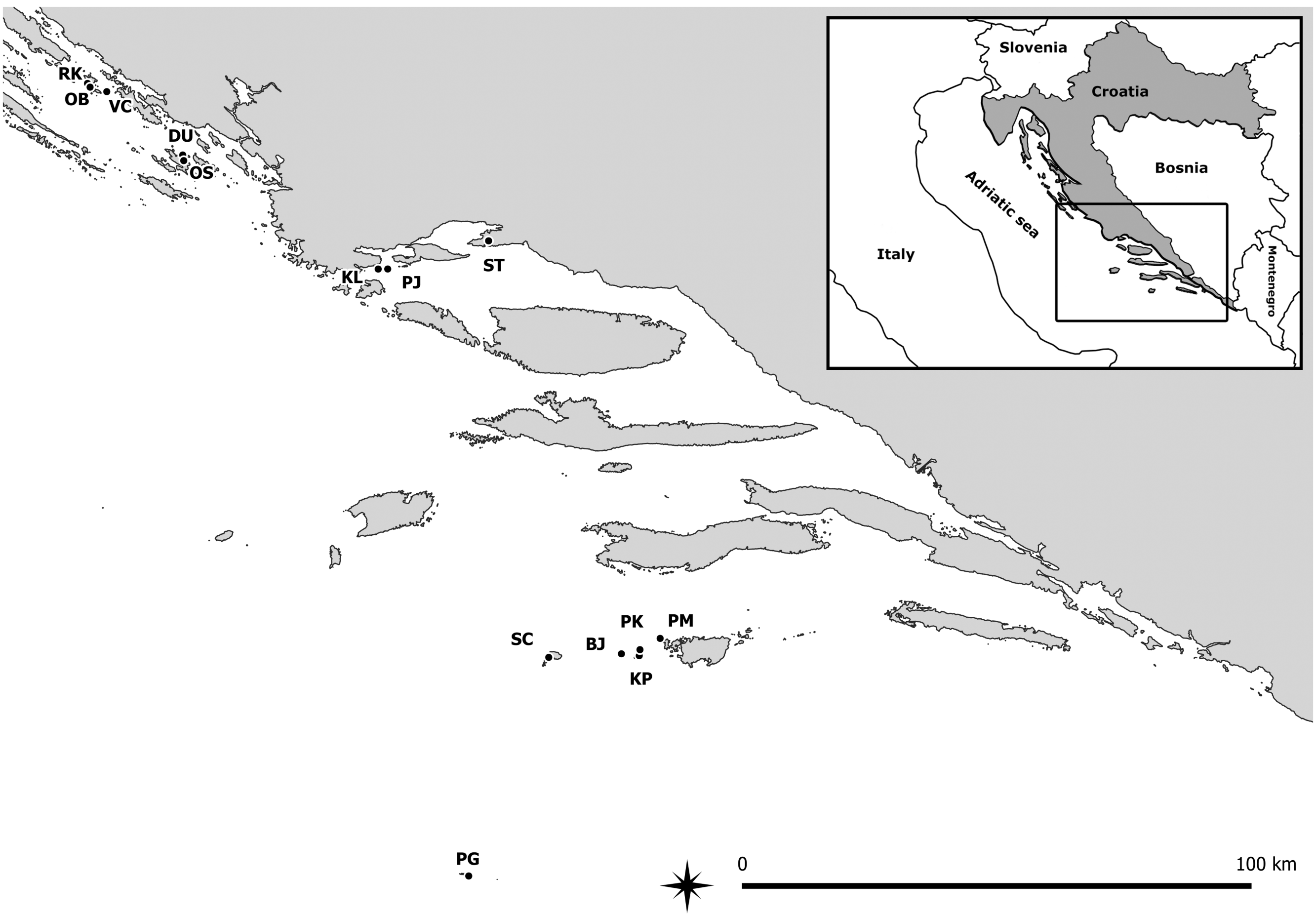

FIGURE 1 Map of the 14 sampling locations of wild *P. siculus* populations: BJ, Bijelac; DU, Veliki Dupinić; KL, Kluda; KP, Kopište; OB, Obrovanj; OS, Oštrica; PG, Mala Palagruža; PJ, Pijavica; PK, Pod Kopište; PM, Pod Mrčaru; RK, Rakita; SC, Sušac; ST, Split; VC, Visovac.

In this study, we combined genomic and quantitative genetic approaches to determine the relative role of adaptive evolution and plasticity in driving rapid phenotypic evolution of Pod Mrčaru *P. siculus*. Specifically, we: (1) quantified genome-wide divergence between the ancestral and the transplanted population; (2) determined adaptive role of a substantial number of highly diverged loci, with the prediction that those loci will be associated with divergent phenotypic traits, or environmental variation in multi-population framework; (3) tested if phenotypic differentiation between populations persists when individuals are raised in a common environment; and (4) quantified heritable variation underlining rapidly diverging traits to determine if they possess enough additive genetic variance to evolve in response to selection.

2 | MATERIALS AND METHODS

2.1 | Experimental design

To estimate the signature of founder event on genetic diversity of newly established Pod Mrčaru (PM) population and to quantify its divergence from the ancestral Pod Kopište (PK) population, we analysed genotype by sequencing data of PM and PK populations and compared the patterns with those observed across 14 *P. siculus* wild populations (Figure 1). Then, we inferred adaptive nature of the highly differentiated PK-PM loci by assessing their association with PK-PM diverged phenotypic traits and their involvement in adaptation processes across 14 wild population. Third, we performed within- and between-PK and PM population crossing experiment to test for the persistence of phenotypic divergence in common garden and assess the additive genetic variance underlying traits of interest. The research and sampling conducted within this study were executed following European and Croatian legislative guidance and were approved by the Ethical Committee of the Biological Department, University of Zagreb, and Croatian Ministry of Environmental Protection and Energy (UP/I-612-07/16-48/116, UP/I-612-07/17-48/06, UP/I-612-07/18-48/21).

2.2 | Genome assembly

The genome of *P. siculus* was assembled de novo from a female *P. siculus* individual from Pod Mrčaru islet. We generated sequencing libraries using the 10× Genomics Chromium Library Preparation and sequenced them on an Illumina HiSeq 4000 sequencer. We then assembled the genome using *supernova mkfastq* run and evaluated the completeness of our genome assembly with BUSCO using the tetrapod database. Finally, we ran BLAST with all assembly scaffolds as queries against the NCBI database to remove any scaffolds with possible contaminants. We used R package *taxonomizr* to assign taxonomy for each alignment hit and removed scaffolds that did not find a BLAST hit to Squamata from the final assembly. For more details see Supplementary Materials and methods.

2.3 | Data collection and genotyping

In summer of 2016 and 2019 we sampled 14 *P. siculus* populations from the Croatian coast of Adriatic Sea, including the two focal islands Pod Mrčaru and Pod Kopište (Figure 1). Individuals from the Pod Mrčaru and Pod Kopište islands were additionally sampled in 2017 and 2018 (and later used in a crossing experiment). For individuals sampled in 2016 and 2019 we collected a set of 14 different phenotypic measurements in situ (Table S1). We further obtained a set of 8 different environmental variables for each sampled site from WorldClim online database and previously published literature sources (Table S2). We performed vegetational surveys on Pod Kopište and Pod Mrčaru, which indicated distinct differences in floral composition, and ecological variation between the two insular habitats (Tables S3 and S9). We have further quantified prey availability on Pod Kopište, Pod Mrčaru and Kopište islands using a standard number of pitfall traps (12) left on each island for 48 h and standardized, timed sweep samples (40 min of sampling covering the different vegetation types; Tables S10 and S11). Shannon diversity and evenness indices indicated that whereas the largest island Kopiste has the greatest diversity and evenness, the smallest island, Pod Mrčaru has overall the lowest diversity in terms of mass and numerical abundance of particular taxa (Table S12). For more details see Supplementary Materials and methods and Supplementary Results.

We genotyped 585 individuals from 14 wild *P. siculus* populations, as well as lizards from the common garden experiment using a genotyping by sequencing approach. We prepared custom-made double-digest sequencing libraries (Table S4) and sequenced them on Illumina HiSeq X Ten platform. We trimmed raw reads of residual adaptor and/or barcode contamination and standardized them in length using custom-made Perl scripts. Reads with uncalled bases and/or cut sites containing more than one mismatch were removed, and those with average Phred quality score below 20 were discarded using the *process_radtags* program in Stacks. We mapped processed reads on the assembled *P. siculus* genome using default settings in the Bowtie2 software. Variant sites were called following the *ref_map* pipeline from Stacks. We discarded the reads with a minimum mapping quality lower than 20. Only the first SNP on each locus was called. We filtered out single nucleotide polymorphisms (SNPs) with a minimum allele frequency lower than 0.05 and heterozygosity higher than 0.6. We restricted the analyses only to SNPs present in all populations, in >60% of individuals in a single population, and in >70% of individuals across all populations. We filtered out variant sites with mean coverage depth lower than 4× and larger than 20×, removed loci with more than 25% of missing data and then imputed population's most frequent known genotype for any remaining missing values. The final dataset consisted of 39,905 SNPs genotyped across 585 *P. siculus* individuals (Table S5), of which 12,381 were polymorphic in PK and PM populations. For more details see Supplementary Materials and methods.

2.4 | Genomic diversity and differentiation

For analyses of genomic diversity and divergence, we removed from the full genomic dataset loci in linkage disequilibrium (LD, $r^2 < .5$) and out of Hardy–Weinberg equilibrium ($p < .05$), resulting in dataset of 21,074 SNPs (of which 9740 SNPs were polymorphic in Pod Kopište and Pod Mrčaru populations sampled across 3 years). For estimation of genomic diversity indices and effective population size, the dataset was further randomly subsampled to a maximum of 19 samples per population (to account for the effect of sample size). Allelic richness (A_R) and observed and expected heterozygosity (H_o and H_e respectively) were assessed using the R package *diveRsity*, nucleotide diversity (π) was estimated using VCFtools software, and inbreeding coefficient (F_{IS}) using Arlequin software. Effective population size (N_E) for each sampled site was calculated using the LD method with random mating in NeEstimator.

Pair-wise F_{ST} indices were calculated using R package *StAMPP*. Genomic divergence among 14 wild populations and between PK and PM populations sampled across 3 years was further examined using a principal component analysis (PCA) of allele frequencies with the R packages *StAMPP* and *adegenet*. We used Bayesian software fastSTRUCTURE to infer ancestral genomic components in 14 wild populations, as well as in all wild Pod Mrčaru and Pod Kopište individuals and their offspring. Recent migration rates among wild populations were estimated using BayesAss approach in BA3-SNPs software. For more details see Supplementary Materials and methods.

2.5 | Adaptive nature of Pod Mrčaru and Pod Kopište genomic divergence

The main presumption of genome scan methods used to identify loci departing from neutral pattern is that the analysed populations are characterized by mutation-drift equilibrium. However, populations that have undergone a recent bottleneck – such as *P. siculus* population on Pod Mrčaru – usually suffer from nonequilibrium demography. Thus, in order to bypass this concern, we first employed genome scans to pinpoint loci that showed distinct allele patterns in Pod Mrčaru and Pod Kopište populations without directly assessing if these patterns are driven by genetic drift or environmental selection. We used three different methods to identify highly diverged, potential 'outlier' loci: non-hierarchical analysis of joint distribution of F_{ST} and heterozygosity from the software Arlequin; Bayesian F_{ST} outlier test based on Dirichlet-multinomial model for allele frequencies from BayeScan software; and a multivariate analysis of outlier loci with respect to population structure implemented in the R package *PCAdapt*. Using the datasets from three sampling years as biological pseudoreplicates (PKPM2016; PKPM2017; and PKPM2018), we chose the loci that were identified by at least two genome scan methods used in at least two out of three yearly comparisons (Figures S14 and S15). Those loci were named 'PKPM outliers' throughout the manuscript, but by the term outlier we refer here to loci which deviate from general distribution, without assuming their neutrality. We then investigated possible adaptive nature of those loci by examining their representation in loci putatively under selection and/or loci associated with environmental variance across 12 wild *P. siculus* populations (excluding PM and PK), as well as their association with diverged phenotypic traits in PM and PK populations. For more details see Supplementary Materials and methods.

We pinpointed outlier loci putatively under selection in 12 wild *P. siculus* populations using the XtX statistic from the software BayPass (Figure S5). We calibrated the thresholds for the XtX statistic outlier detection using pseudo-observed datasets with 10,000 SNPs and verified similarity among covariance matrices obtained on empirical and simulated datasets using Forstner and Moonen distances (FMD < 1). We further confirmed that covariance matrices obtained from BayPass models manifested high correlation with the matrix of 12 *P. siculus* population pairwise F_{ST} values (Mantel $r = -.93$, $p = .0001$), indicating adequate approximation of population structure. We then explored genotype-environment associations using the auxiliary model implemented in the software BayPass. SNPs considered strongly associated with environmental variation were those with BF values >20 dB (deciban units) (Figure S6). This variation among populations was modelled using scores from the first five principal components in the PCA of eight ecological variables related to climate (mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, mean annual precipitation, mean annual solar radiation, and mean annual wind speed), ecological isolation (distance to large island), and area of the island (Table S2, Figure S3). The role of the same ecological covariates in the multi-population differentiation was further interrogated by partitioning phenotypic and genomic variance between spatial and ecological components for 14 populations (Figure S4) using a multivariate redundancy analysis (RDA) approach implemented in the R package *vegan*. Geographical variation was modelled using the first two dbMEM vectors obtained from distance-based Moran's eigenvector analysis. Genotype data was expressed as a matrix of population allele frequencies, and for phenotypic response matrix we used scores from the first five principal components from PCA of phenotypic variables.

We used a latent factor mixed models (LFMM) analysis implemented in the R package *lfmm* to explore genotype–phenotype associations (GPA) in our two focal populations phenotyped in 2016. We fitted LFMM models with two latent factors ($K = 2$) and recalibrated the obtained z-scores with modified genomic inflation factors to obtain a uniform p-value distribution which is expected under the null-hypothesis (Table S6). Loci showing significant association with analysed phenotypic variables were determined by a Benjamini-Hochberg procedure on adjusted *p*-values with false discovery rate (FDR) = 0.05 (Figures S7–S10). For more details see Supplementary Materials and methods.

2.6 | Crossing experiment in the common garden

In order to assess evolutionary potential in rapidly diverged phenotypic traits connected to head size and shape in our two focal populations, we conducted a 4-year-long crossing experiment in a common garden. We sampled adult *P. siculus* individuals on Pod Mrčaru and Pod Kopište islands in March of 2017 and 2018 and brought them to Zagreb Zoo where we set controlled crossings both within and between ancestral and transplanted population. Parental and juvenile generations were kept and raised in identical conditions and fed on the same cricket-based diet. We obtained extensive data on 7 phenotypic traits of the head and body (Figure 2) by photographing the experimental individuals (68 F0, 85 F1 and 5 backcross) and processing the photographs with image analysis software ImageJ to obtain phenotypic measures of interest using standard geometric morphometry based on landmark data and custom-made scripts in R. The repeatability of the phenotyping across both image analysis and photographing was adequate for all analysed traits (Table S7) and measures obtained using image analysis and traditional calliper-based phenotyping approach were found to be significantly correlated (Table S8). Additionally, we measured bite force in a subset of individuals from the crossing experiment (54 F0 and 75 F1 individuals), using a Kistler force transducer set in a custom-built holder and connected to a Kistler charge amplifier (Herrel et al., 1999). We assessed phenotypic differentiation in the F0 generation and F1 and backcross offspring raised in the common garden using simple t-test and analysis of variance approach in R. To evaluate whether the pattern of phenotypic differentiation in Pod Kopište and Pod Mrčaru persisted in the wild, we graphically compared raw population mean trait values obtained for Pod Mrčaru and Pod Kopište individuals in 2006 and published by Herrel et al. (2008) to those obtained for F0 individuals in our experiment. We further used quantitative genetic analysis of phenotypic traits connected to head size and shape, conducted using Bayesian animal models in *MCMCglmm* R package with group-specific additive genetic variance to assess the additive genetic variance and estimate heritability in our traits of interest. We derived the T^{-1} and D^{-1} components from the Cholesky decomposition of inverse A^{-1} relatedness matrix directly from the pedigree and then scaled them by the respective group-proportions to obtain group-specific A^{-1} relatedness matrices for each genetic group. We also included a matrix with genetic group proportions for each individual (Q) as a fixed effect in the model to account for potential differences in mean breeding values between individuals from different genetic groups (Wolak & Reid, 2017). Heritability (h^2) was calculated from posterior estimates as the ratio of additive genetic variance component to total phenotypic variance. For more details see Supplementary Materials and methods.

3 | RESULTS

3.1 | Genome assembly

We generated a highly contiguous *P. siculus* genome assembly with contig and scaffold N50 of 75.56 Kb and 37.45 Mb, respectively, and 96.43% of base pairs (1.33 Gb) in scaffolds longer than 10 kb (Table S13). Genome quality after filtering showed high completeness with 94.9% complete BUSCOs in the tetrapod database (for more details see Supplementary Materials and methods).

3.2 | The newly established Pod Mrčaru population shows genome-wide differentiation from the ancestral Pod Kopište population and weak genetic erosion

We observed genome-wide divergence of the newly established Pod Mrčaru (PM) population from its ancestral counterpart at Pod

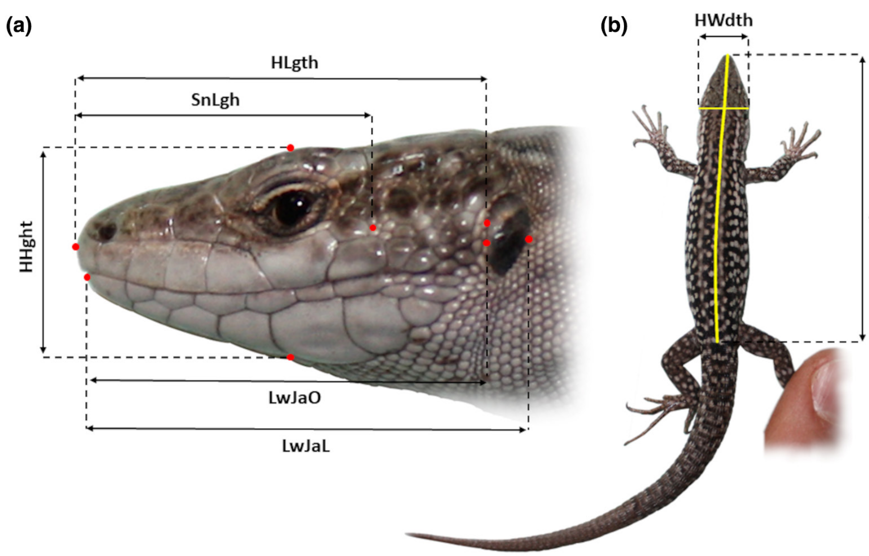

FIGURE 2 Phenotypic measures collected for lizards from the common garden experiment from images of: (a) lateral side of the head (HHgth, head height; HLgth, head length; LwJaL, lower jaw length; LwJaO, lower jaw outlever; SnLgh, snout length) and (b) dorsal side of the body (HWdth, head width; LtHip, length to hip).

Kopište (PK) 45 years after the introduction into the new environment. Principal component analysis (PCA) of allelic frequencies displayed complete separation of PK and PM populations (sampled in three consecutive years) along the first principal component, which explained modest 3.35% of genomic variance (Figure 3a). Genomic differentiation was confirmed by pairwise F_{ST} reaching a value of 0.045 (Table S14). While this is the lowest value recorded for any pairwise comparison of sampled wild populations, it is still comparable to differentiation rate observed between some other long-term isolated insular populations in the area (0.071 and 0.077; pairwise comparison between populations Kopište (KP) and Sušac (SC), and between Kopište (KP) and PK, respectively, Table S14). Furthermore, analysis of individual ancestry based on variational Bayesian inference demonstrated a clear distinction of PK and PM ancestral genomic components in individuals sampled on the islands and intra- and inter-population F1 crosses from the common garden experiment (Figure 3b).

In the multipopulation framework, the common genetic ancestry and low genomic divergence between PK and PM populations became more evident (Figures S11 and S12). We did not detect any signal of recent inter-insular migration in terms of PM individuals showing genomic introgression from PK or any other population. The lack of recent population migration among islands was confirmed by the *BayesAss* analysis, where none of the estimated pairwise population migration values were significantly different from zero (Table S15).

Lower genetic diversity was recorded for populations inhabiting southern islands, including Pod Mrčaru and Pod Kopište (Table S16, Figure 1). In comparison to the ancestral population on Pod Kopište islet, weak genetic erosion in PM population was evident across all three sampling years, with average decrease of 2% in allelic richness, 1% in nucleotide diversity and 8% in observed heterozygosity. Nonetheless, recently founded PM population exhibited higher genetic diversity across all measured indices than the population on islet Bijelac (BJ) in the same archipelago. Neither of the genetic diversity indices correlated with the island area ($p > .05$), and populations on some small islands harboured substantial amount of genetic variation (e.g. Rakita (RK) and Dupinčić (DU), Table S16). Among all populations, PK and PM had the lowest observed (and insignificant) inbreeding coefficients (F_{IS}). PM population exhibited higher number of rare alleles than PK across all three studied years (Figure S13). Effective population size (N_E) of both PK and PM populations varied across the sampling years, but fluctuation was more pronounced in PK population. Estimated N_E values of both populations were in similar range in 2016 and 2017 (220 ± 18.3 to 365.3 ± 40.7 for PK, and 230.3 ± 16.3. to 318.9 ± 4.2 for PM), while in 2018 N_E of PK population increased to 618.6 ± 132.2 (Table S16). Yet, effective population size estimates on the Pod Mrčaru islet were comparable to those recorded on some much larger islands (Kopište (KP) and Sušac (SC), Table S16). Although N_E did not correlate with the area across all populations, it did across 11 islands smaller than 0.08 km^2 (Spearman rank correlation rho = 0.64, $p < .05$). To infer how the obtained effective population size relates to the number of actual contributing parents across our data for PM and PK populations, we further calculated N_E for the F1 crosses and obtained N_E values similar to the known number of parents (F0) (Table S16).

3.3 | Highly diverged loci show a putatively adaptive role

We identified 116 loci for which distinct allelic differentiation was observed between PK and PM populations using three genome scan methods (Figure S16). As the demographic history of the PM population does not imply mutation-drift equilibrium, we could not properly test for deviations from neutrality and parse the effects of genetic drift and putative selection on patterns of per locus genomic divergence. Thus, we refer to those loci as 'PKPM outliers' in the following text. The average F_{ST} value between PM and PK populations for those 116 'outlier' loci was 0.244 across three sampling years, which is notably higher than the genome-wide average of 0.045. None of the loci reached fixation, and there were no private alleles detected in the PM population. We then investigated the possible adaptive role of these 'PKPM outliers' within 12 wild *P. siculus* populations (excluding PM and PK), and their representation among loci associated with diverged phenotypic traits in PM and PK populations.

Across 12 wild *P. siculus* populations (excluding PK and PM populations) 678 out of 39,883 loci were classified as putatively under selection using the BayPass core model, and 592 of them showed signal of directional selection. In the genotype-environment association (GEA) analysis using the genotype dataset for the same 12 populations, 4431 unique loci were found to be associated with principal components of environmental variation (Bayes factor > 20) (Table S17). Overlap between 116 PKPM 'outliers' and those 4431 GEA loci showed that 21.6% (25 out of 116) 'PKPM outliers' were also associated with environmental variation in the independent dataset of 12 other populations (Figure 4). Five 'PKPM outliers' loci were pinpointed as both associated with the environment and as putatively under selection across 12 other *P. siculus* populations (multipopulation outliers, Figure 4).

Genotype–phenotype association (GPA) analysis based on latent factor mixed model resulted in 1075 unique loci associated with male and/or female phenotypic traits in PM and PK populations, including those related to head size and shape (Table S18). Thirty of the 116 'PKPM outliers' (25.86%) were among the loci associated with the phenotype in PK and PM populations (Figure 4). Overall, 51 of 116 'PKPM outliers' (43.97%) were picked up by at least one, and 8 (6.9%) by at least two analytical approaches used to infer their adaptive role. We further found that 17.49% of the loci associated with phenotypic traits in PK and PM populations were also pinpointed as multipopulation outliers or environmentally associated loci in the independent dataset of 12 other *P. siculus* populations (Figure 4). All detected overlaps among 'PKPM outliers', loci found as putatively under selection (multipopulation outliers) or those associated with environmental variation among 12 *P. siculus* populations (GEA), and

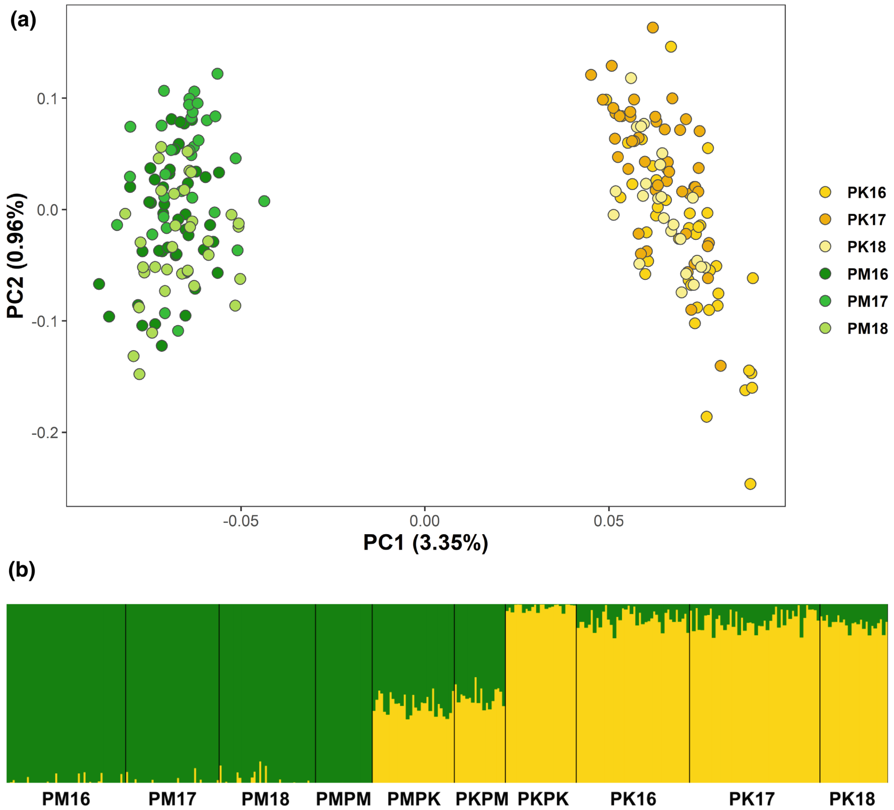

FIGURE 3 Genomic divergence between the ancestral Pod Kopište (PK) and the introduced Pod Mrčaru (PM) population: (a) principal component (PC) analysis of allele frequencies in native PK and PM populations sampled across 3 years (2016, 2017, 2018); (b) Bayesian inference of ancestral genomic components in PK and PM population and intra- (PKPK, PMPM) and inter-population (PKPM, PMPK) F1 crossings, computed with software *fastStructure* ($K=2$).

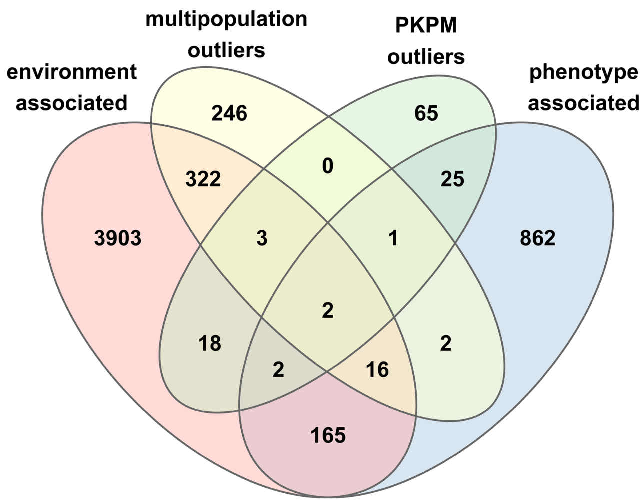

FIGURE 4 Adaptive nature of highly diverged loci between Pod Kopište and Pod Mrčaru populations: overlap of 116 'PKPM outlier' loci with the loci associated with diverged phenotypic traits in Pod Mrčaru and Pod Kopište *P. siculus* populations (phenotype associated), the loci identified as putatively under directional selection (multipopulation outliers) and the loci associated with the environmental variation (environment associated) across independent set of 12 other wild *P. siculus* populations. All pairwise overlaps are significant ($p<.0000001$).

loci associated with PK-PM diverged phenotypic traits (GPA), were higher than could be expected purely by chance ($p<.0000001$).

The role of ecological covariates in multi-population genomic differentiation was confirmed using multivariate redundancy analysis (RDA). Partitioning of genomic variance conducted using all 39,905 polymorphic loci in *P. siculus* dataset revealed that 18.89% of total genomic variance could be explained by ecological factors after controlling for spatial structure, while only 3.94% was explained by geographical distance after controlling for ecological variation among sampling sites (Table S19). The joint influence of ecological and geographical components was high and accounted for 36.21% of total genomic variance, which reflects correlations between spatial and ecological factors. Similarly, ecological factors explained 13.6% of male and 8.29% of female phenotypic variance after accounting for geographic distances, while partial RDA geographic model (after accounting for ecological covariates) explained only 1.73% of variance in males and was insignificant for females (Table S20).

3.4 | Diverged phenotypic traits have moderate heritability, but are plastic in the common garden

The patterns of phenotypic divergence between the ancestral PK and the transplanted PM population observed in 2004–2006 (Herrel et al., 2008) remained stable over the course of 11 years (Figures S17 and S18), with individuals from Pod Mrčaru islet having significantly larger heads and bodies than individuals from Pod Kopište (Figure 5a). Conversely, results of the intra- and inter-population crossing experiment show that this differentiation did not persist in the F1 and backcross offspring raised in the common garden (Figure 5b), indicating that phenotypic differences between PM and PK populations are largely driven by phenotypic plasticity and/or

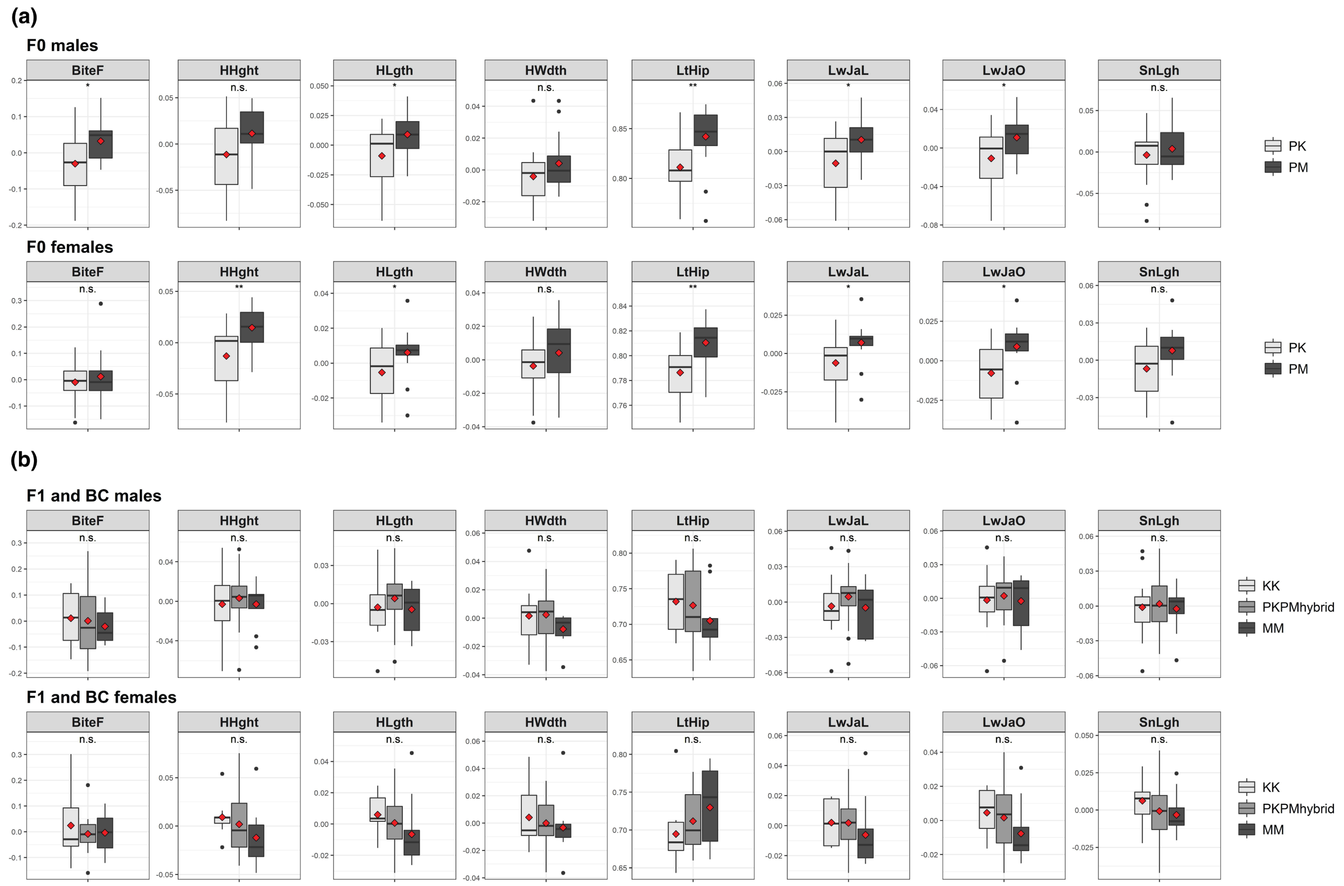

FIGURE 5 Phenotypic trait variability in male and female F0 individuals from Pod Kopište (PK) and Pod Mrčaru (PM), and F1 and BC individuals from common garden crossings: Crosses are denoted as KK = PK♂ + PK♀, MM = PM♂ + PM♀, PKPMhybrid = PK♂ + PM♀ or PM♂ + PK♀. Red rhombus indicates group mean, bold line stands for median, the box represents quartiles and whiskers stand for minimum and maximum recorded values. Pairwise *t*-test or ANOVA significance is indicated above boxplots (**<.01, *<.05, n.s. = not significant). Phenotypic trait codes are defined in Figure 2 and Table S1.

genotype by environment interactions. Nonetheless, quantitative genetic analysis pointed towards moderate heritability of bite force ($h^2 = 0.28$), morphometric traits related to lizard head size and shape ($h^2 = 0.42–0.51$), and body size ($h^2 = 0.35–0.37$) (Table 1). Likewise, the amount of estimated additive genetic variance in Pod Mrčaru and Pod Kopište genetic groups was not significantly different (posterior distribution of differences in variances is practically equivalent to zero), indicating the absence of bottleneck-related genetic erosion of additive genetic variance underlying the divergent traits in the PM population.

4 | DISCUSSION

Systems that are still in the early phases of ecotype formation are particularly well suited to investigate the genomic patterns underlying rapid adaptive evolution (Soria-Carrasco et al., 2014). In this study we leverage the relatively well-known colonization history and ecologically induced phenotypic divergence of *P. siculus* population on the island of Pod Mrčaru to study the evolutionary events driving rapid phenotypic shifts in populations encountering novel isolated environments. Perceiving this case study of contemporary adaptation within the multi-population framework further facilitated the comparison of the evolutionary shift in PM population induced by anthropogenic introduction with demographic and environmentally driven patterns among wild populations.

Genetic diversity of newly founded populations is a major factor contributing to its colonization success and is largely determined by the number of founders, genetic diversity of source population and the subsequent demographic trends (especially changes in population size and migration rates) (Crawford & Whitney, 2010; Forsman, 2014; Szűcs et al., 2017). The observed decrease in genetic diversity of PM population is modest in relation to average values reported for populations invading new habitats (Dlugosch & Parker, 2008). This implies that the founding event did not cause strong genome-wide genetic erosion, despite the very limited number of individuals contributing to the gene pool of the new population. Likewise, these results also suggest that the PM population did not experience any additional major bottlenecks. Various studies on newly founded populations report subsequent inflation of their genetic variance through introgressions or multiple introductions (e.g. Fuller et al., 2020; Kolbe et al., 2004). Our results show no

TABLE 1 Posterior mean estimates of variance components and heritability (h^2) for the two genetic groups (Pod Kopište = PK; Pod Mrčaru = PM).

	BiteF	HHgth	HLgth	HWdth	LwJaL	LwJaO	SnLgh	LtHip
$V_P \times 10^3$ [CI]								
PK	9.16 [6.35–12.41]	1.16 [0.8–1.57]	0.55 [0.38–0.74]	0.5 [0.36–0.67]	0.6 [0.42–0.81]	0.7 [0.49–0.94]	0.78 [0.55–1.05]	1.82 [1.25–2.44]
PM	9.25 [6.11–12.98]	1.04 [0.73–1.38]	0.52 [0.37–0.7]	0.49 [0.34–0.65]	0.58 [0.41–0.77]	0.64 [0.46–0.86]	0.68 [0.48–0.91]	1.9 [1.28–2.6]
$V_E \times 10^3$ [CI]	6.49 [4.19–8.99]	0.6 [0.38–0.83]	0.26 [0.18–0.35]	0.26 [0.17–0.34]	0.3 [0.2–0.41]	0.35 [0.23–0.47]	0.38 [0.25–0.51]	1.17 [0.79–1.57]
$V_A \times 10^3$ [CI]								
PK	2.66 [0.29–5.82]	0.56 [0.19–1.02]	0.29 [0.13–0.48]	0.25 [0.11–0.41]	0.3 [0.13–0.51]	0.35 [0.14–0.6]	0.4 [0.16–0.69]	0.65 [0.17–1.28]
PM	2.75 [0.2–6.57]	0.44 [0.15–0.77]	0.26 [0.12–0.44]	0.24 [0.11–0.4]	0.28 [0.12–0.45]	0.29 [0.12–0.48]	0.3 [0.13–0.51]	0.73 [0.18–1.43]
V_A [CI]								
PK-PM	-9.06e-05 [−0.0049–0.0049]	1.23e-04 [−0.0004–0.00066]	2.6e-05 [−0.00022–0.00028]	9.68e-06 [−0.00022–0.00023]	2.47e-05 [−0.00024–0.0003]	5.78e-05 [−0.00024–0.00038]	1.01e-04 [−0.00023–0.00045]	-7.4e-05 [−0.0011–0.00085]
h^2 [CI]								
PK	0.28 [0.05–0.54]	0.47 [0.24–0.71]	0.51 [0.33–0.71]	0.48 [0.3–0.67]	0.49 [0.29–0.69]	0.49 [0.29–0.7]	0.51 [0.3–0.71]	0.35 [0.13–0.58]
PM	0.28 [0.04–0.56]	0.42 [0.21–0.63]	0.49 [0.31–0.67]	0.47 [0.29–0.66]	0.47 [0.28–0.65]	0.45 [0.27–0.64]	0.44 [0.25–0.63]	0.37 [0.15–0.61]

Note: Total phenotypic variance (V_P) is partitioned into additive genetic (V_A), and environmental or residual (V_E) components. Environmental component estimates are the same for both genetic groups. V_A [CI] PK-PM marks the difference in posterior V_A distribution between genetic groups.

Abbreviations: BiteF, bite force; HHgth, head height; HLgth, head length; HWdth, head width; LtHop, length to hip; LwJaL – lower jaw length; LwJaO – lower jaw out-lever; SnLgh, snout length.

evidence that the gene flow was considerably replenishing the genetic diversity of PM population, as neither the estimates of recent migration rates nor the analyses of ancestral genomic components point to existence of immigrants or PM individuals of mixed ancestry. Nevertheless, *Podarcis* species are known for their propensity to hybridize in both their old and the more recent evolutionary history, and *P. siculus* is no exception (Capula, 2002; Gaczorek et al., 2023; Yang et al., 2021). Thus, due to our limited genomic insights, we cannot completely rule out the possibility of hybridization between the newly translocated *P. siculus* and native *P. melisellensis* populations in the short time of their coexistence on Pod Mrčaru island, but we consider this event to be unlikely.

The lack of correlation between genetic diversity indices and island area, along with ample amount of standing genomic variation observed in some populations on small islands, suggests that genetic diversity of insular *P. siculus* is less defined by the island size than by source population and prior evolutionary and demographic processes. Although the number of founders on Pod Mrčaru islet was particularly small – only 10 *P. siculus* individuals (Gorman et al., 1972), field surveys suggested higher population density of *P. siculus* on Pod Mrčaru than on Pod Kopište (Herrel et al., 2008; Vervust et al., 2009). In line with those observations on census population size, we obtained similar estimates of N_E on Pod Kopište as on the ~ three times smaller Pod Mrčaru islet. On the other hand (and unlike genetic diversity), effective population size was found to be limited by small islands area across multiple populations. This result suggests that the current PM population is relatively large and with high fitness. Comparatively large population size, modest loss of genetic variation, and swift competitive success, all point to rapid initial population growth of PM population after the founding event. It has been suggested that a fast increase in population size has a potential to limit the amount of genomic variation lost during a bottleneck (Allendorf, 1986; Kirkpatrick & Jarne, 2000; Murphy et al., 2015). A recent population expansion could also have led to an excess of rare variants (Keinan & Clark, 2012; Maruyama & Fuerst, 1985). This might likewise be an underlying cause of the smaller decrease in allelic richness than in heterozygosity observed in PM population, which deviates from common expectations of bottleneck effects on genetic diversity (Nei et al., 1975). Relatively high amount of retained genetic variance could be additionally driven by other subtle evolutionary mechanisms, such as associative overdominance that may promote the maintenance of neutral genetic variation in small populations experiencing bottleneck (Schou et al., 2017).

In <25 generations, the introduced PM population has diverged at the genome-wide level from the source population, reaching >60% of the differentiation observed between the long-term isolated insular populations on Pod Kopište and Kopište (the next closest island inhabited by *P. siculus*). While the widespread genomic divergence is consistent with the neutral expectation of genetic drift propelled by a small number of founders and lack of gene flow (Sendell-Price et al., 2021), both drift and selection are expected to contribute not only to genomic but also to phenotypic differentiation of small populations invading different habitats (Colautti & Lau, 2015; Keller &

Taylor, 2008; Kolbe et al., 2012). Even the good alignment between the phenotypic change detected in the PM population and the observed ecological shift of lizards on Pod Mrčaru (Herrel et al., 2008) cannot completely exclude the possible role of phenotypic drift, nor allow us to discriminate between adaptive genetic evolution and adaptive phenotypic plasticity.

Considering that none of the methods utilized to pinpoint 'PKPM outlier' loci was specifically designed to account for non-equilibrium conditions involved in the translocation experiment and bottleneck that PM population experienced at the time of its introduction (Excoffier et al., 2009; Foll & Gaggiotti, 2008), their putatively adaptive nature was inferred indirectly. Nonetheless, complementary insights into substantial number of 'PKPM outlier' loci being associated with ecologically pertinent diverged traits and found relevant for adaptive evolution across multiple populations indicate adaptive nature of their differentiation. Given that our methodology offers only limited and partial insights across the genome, it is impossible to infer if any of the adaptive signals stem from direct selective pressures on investigated loci, or whether those loci only reflect adaptive genomic responses in linked genomic regions through the hitchhiking effect (Nosil et al., 2009). Additionally, a large proportion of loci with above-average PK-PM F_{ST} values showing generally neutral patterns of allelic frequency change are also indicative of genetic drift contributing to genome-wide population divergence.

Our results support the arguments for partial genetic basis of the studied phenotypic traits. Moreover, they point to an evolutionary parallelism in genetic basis of adaptation in the introduced and wild populations and are thus unlikely to reflect merely stochastic genetic drift. Considerable environmental impact on phenotypic and genomic divergence across populations was additionally implied by ecology having higher explanatory power than geographic distances in RDA analyses. However, in such studies it is difficult to pinpoint the association between specific phenotypic traits and specific environmental factors. Firstly, the signal of ecological impact on populations' phenotypic (and genotypic) divergence might stem as well from natural selection on other, likely correlated, yet unanalysed phenotypic traits. Furthermore, the variances in climate factors, island area, and ecological isolation, utilized in genotype-environment association analysis, are not only expected to exert selective pressures on populations directly, but also through considerable modulation of biotic components of insular ecosystems (Mueller-Dombois, 1992; Novosolov et al., 2016; Veron et al., 2019), and thus the effects of unmeasured cofounding abiotic variables may be at play. Lizards translocated on Pod Mrčaru encountered an ecologically distinct habitat with a different vegetational composition and somewhat different prey availability. The vegetational cover is expected to influence microclimatic conditions, temperature, solar exposure, wind exposure, moist availability, but also shelter availability and predator exposure, prey variance and abundance, basking opportunities, etc. Among the employed environmental covariates, temperature has a particularly important influence on biology and life history of *P. siculus* (Senczuk et al., 2017) and is known to drive the thermal ecology of *Podarcis* lizards on small islands (Pafilis et al., 2019). Even though effective thermoregulation is achieved along *P. siculus* colonization range (Burke & Ner, 2005; Kapsalas et al., 2016), lizard thermoregulatory behaviour and performance can as well be the subject of natural selection (Logan et al., 2018).

Genome-wide distribution and number of loci associated with phenotypic variation or having putatively adaptive role in the novel lizard population on Pod Mrčaru are indicative of polygenic selection affecting allele frequency distribution across multiple loci underlying adaptive quantitative traits (Fuller et al., 2020; Perreault-Payette et al., 2017; Rellstab et al., 2015). These results are congruent with the scenario of adaptation from standing genetic variation, which is considered to be faster than adaptation from de novo mutations and more likely to ensue in early stages of population establishment (Barrett & Schluter, 2008; Crisci et al., 2016). Nevertheless, our reduced genomic approach did not allow to completely exclude the potential role of novel mutations.

The results of the common garden experiment point to moderate heritability of bite force and phenotypic traits related to head size and shape in lizards from Pod Mrčaru and Pod Kopište, confirming those traits show enough additive genetic variance to evolve under selection in both populations. This is in agreement with our recent work showing that not only intra- but also inter-specific patterns of head size and shape in insular *Podarcis* lizards are driven by variation in ecological conditions, and thus widely subjected to natural selection (Taverne et al., 2019). Moreover, no significant erosion of additive genetic component was observed in PM population. Both theory and experimental findings support that additive genetic variation for ecologically important traits does not necessarily follow a decrease in neutral genetic diversity in populations that have undergone bottleneck (Estoup et al., 2016), and can even increase if nonadditive genetic variance translates into additive, for example, due to epistasis or dominance (Santos et al., 2012; Van Buskirk & Willi, 2006). Additionally, head shape and size are considered to be under sexual selection in *P. siculus* (Taverne et al., 2020), which may further support the maintenance of genetic variance underlying those traits (Radwan et al., 2016).

Heritable nature of differentiated traits coupled with adaptive role of diverged loci is indicative of rapid evolutionary response to new ecological conditions encountered on Pod Mrčaru. Conversely, the crossing experiment revealed a lack of persistence of differences between populations in F1 generation, which confirms the ongoing plasticity of focal traits in PM population. However, heritability and plasticity are not necessarily mutually exclusive, and variance in most traits is the additive result of the combined effect of genetics and environment on the phenotype (Visscher et al., 2008). The lack of difference among phenotypic distributions in offspring groups raised in the common garden environment indicates that the part of variance which is evident as population phenotypic divergence is governed mainly by plasticity. The estimated heritability thus refers only to the part of the phenotypic variance among individuals that is explained by the genetic component (note that the traits are still variable in the common garden). Overall, our results indicate the alignment of genetic and plastic mechanisms across phenotypic responses to ecological change. At this point we were unable to specifically test two important evolutionary questions: whether there are also genotype by environment interactions at play, and to what extent is such plastic response a feature of the ancestral PK population. Our study system could provide an opportunity to test for the plasticity-first hypothesis (Noble et al., 2019), but would demand another, up to 4 years long, reciprocal crossing experiments in quite challenging experimental conditions with lizards fed an omnivorous diet (with the plant material preferably resembling the one encountered on Pod Mrčaru islet). The epigenomic aspects of PM population differentiation also need to be addressed in future research – epigenomic responses are recognized as important driver of invasion success, can facilitate environmentally induced plastic effects or inflate genetic variation through modulations of transposons activity (Herrel et al., 2020; Marin et al., 2020; Pimpinelli & Piacentini, 2020). Regardless of the exact underlying mechanism, stability of phenotypic divergence between PK and PM population over the course of more than a decade suggests continuous environmental reinforcement. In the initial stage of the founder population settlement on Pod Mrčaru, plasticity could have boosted survival and population growth, at the same time empowering the competitive success of *P. siculus* over *P. melisellensis* through the exploration of alternative trophic resources. Our insights into concurrent plastic and genetic adaptive processes are in line with recent observations of early evolution in lizard cryptic coloration initiated by phenotypic plasticity and accompanied by genomic adaptation (Corl et al., 2018). Such plastic responses, well-adjusted to environmental challenge, have the potential to uncover previously hidden genetic variance and jump-start genomic adaptation (Noble et al., 2019). Studying this remarkable system in its evolutionary infancy demonstrates that additive genetic variance is not necessarily diminished in a population established by a small number of founders and further advances our understanding of intertwined plastic and genetic mechanisms underlying the successful colonization of novel habitats.

AUTHOR CONTRIBUTIONS

AŠ, AH and JS designed the research, AH, AŠ, DL, IS, ÓM and MG collected phenotypic data and samples on the field, ÓM, AŠ, DL, IS, IC and MG performed the crossing garden experiment and phenotyping, TH performed and analysed vegetational and floristic survey, AH performed survey on prey availability, ÓM and IS analysed phenotypic data and IS analysed heritability estimates. DYCB and RN assembled the genome, IS, ÓM, AŠ, MN, and RB performed population genomic analyses. AŠ, IS, AH, ÓM, JS, MEA, MT and MN interpreted the data, AŠ, IS and DYCB drafted the manuscript, and AH, JS, ÓM, MT, MN and MEA revised the draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supporting Information. Individual genotypic and phenotypic data are available on DataDryad (https://doi.org/10.5061/dryad.zkh1893gh). Raw sequence reads are deposited in the SRA (BioProject PRJNA1032101). The assembly genome is stored in GenBank database (accession no. JAXCMG000000000, BioProject PRJNA1032059). Custom-made scripts are uploaded on Github (https://github.com/Stambuk-lab/Sabolic_et_al_2023).

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