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ORIGINAL PAPER

Trait variation in a successful global invader: a large-scale analysis of morphological variance and integration in the brown trout

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Abstract In ecology and evolution, the small population paradigm posits that reduced genetic variation will result in limited phenotypic variation that, in turn, will affect population resilience and potential for adaptation. Over the last decade though, such a paradigm has been questioned, with evidence that mechanisms independent of genetic variation may be also important in shaping phenotypic variation. However, there are few large-scale empirical examples, especially from aquatic ecosystems. Using the large-scale natural experiment afforded by the global invasion of brown trout (*Salmo trutta*), we quantify standing phenotypic variation in morphology among different introduced ranges, relative to the native range. By using shape variation and morphological integration as indicators of phenotypic variation, we show that neither founding population size nor time since founding (i.e., effect of selection regime) are correlated to the amount of morphological variation, contrarily to common expectations. Beyond founding population size and time since founding, the amount of morphological variation is mostly controlled by factors at the population level rather than at the region level, and is not lower in invaded regions compared to the native range. These results suggest that the dynamics of phenotypic variation may be largely independent of population size and mostly determined by site-specific patterns of selection.

Keywords Phenotypic variation · Invasion · Morphological integration · Population size

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Introduction

The dynamics of intraspecific diversity are thought to be tightly related to the amount of available genetic variation (Barrett and Schluter 2008; Lai et al. 2019), especially under environmental change (Hendry et al. 2018; Lande and Shannon 1996). But, theoretically, the amount of genetic variation is decreased in small populations due to the effect of genetic drift (Frankham 1995; Nei et al. 1975). This small population effect on genetic diversity has long influenced predictions for how populations will colonize, persist, spread, and thrive (Mayr 1965). In invasion biology, a common manifestation of this general idea is that propagule pressure (the number and diversity of individuals of a species reaching a new environment) will drive the probability of colonization and expansion, partly due to the amount of genetic variation available for adaptation (Blackburn et al. 2011; Simberloff 2009). Indeed, some evidence exists that invasion success is positively related to the amount of founding genetic variation (Correa and Moran 2017; Crawford and Whitney 2010; Dlugosch and Parker 2008; Forsman 2014; Jones and Gomulkiewicz 2012). Yet a debate persists given the numerous instances of successful invasions arising from only a few founding individuals (Rollins et al. 2013; Roman and Darling 2007).

One potential reason for this apparent disconnection between theory (small founding populations should have very limited adaptive potential) and numerous contradictory empirical outcomes (small founding populations are often very successful) is that neutral genetic variation is not the best predictor of adaptive responses (Ellegren and Sheldon 2008; Frankham 1995; Savolainen et al. 2013). Instead, phenotypic variation—whether genetic or plastic in origin—determines the fit between organisms and the environment (i.e., adaptation), and this phenotypic variation might be poorly predicted by (neutral) genetic variation. That is, even very small populations with limited genetic variation might show high phenotypic variation resulting from complex genetic architectures and diverse environmental influences on development and behaviour (Yates et al. 2019). Thus, the key question might not be "Do small founding populations have limited genetic variation?" but rather "Do small founding populations have limited phenotypic variation?". We address this question through a study of one of the world's most widely introduced fish: the brown trout (*Salmo trutta*).

In its original Eurasian distribution (Fig. 1), brown trout are often at risk of local extinction, and the "small population paradigm" (Caughley 1994) has been repeatedly invoked as contributing to these declines (Antunes et al. 1999; Gil et al. 2016; Vincenzi et al. 2010). This is consistent with the common perception that population declines induce reduced genetic variation and cause inbreeding to the point that populations are at risk of extinction. Paradoxically, the brown trout is also one of the most successfully introduced (Lowe et al. 2000) and impactful invasive species in six continents. Indeed, it is now established in 46 new countries, disturbing local ecosystems (Flecker and Townsend 1994), and affecting native diversity (Budy et al. 2013; Correa et al. 2012; Ortiz-Sandoval et al. 2017; Young et al. 2010; Závorka et al. 2018). Some authors have even argued that the species now occupies nearly all potential suitable habitats at the global scale (Lobón-Cerviá and Sanz 2017; McIntosh et al. 2010). As a result of this widespread introduction and successful establishment, brown trout provide an excellent system for testing whether phenotypic variation (specifically, body shape—see below) is reduced during at least some invasions—especially those founded by few colonizing individuals.

Various aspects of body shape in brown trout, as in all fishes, influence multiple vital functions through diverse interactions with the environment (Langerhans 2008). For instance, the position, size, and orientation of the mouth influence foraging efficiency on different resources (Wainwright 1996). Likewise, body depth and the position and size of fins influence burst and sustained swimming ability (McLaughlin and Grant 1994; Morinville and Rasmussen 2007), predator defense (Domenici et al. 2008) and reproduction (Makiguchi et al. 2017). These and other aspects of body shape show plastic responses to environmental conditions and they are also known to be moderately heritable in brown trout and other salmonids (mean heritability coefficient h^2 of 0.29, based on a review of quantitative genetics, Carlson and Seamons 2008). Indeed, body shape traits have been documented to evolve rapidly when salmonids are introduced into new environments, with examples including body depth in sockeye salmon (Hendry et al. 2000) and snout length in chinook salmon

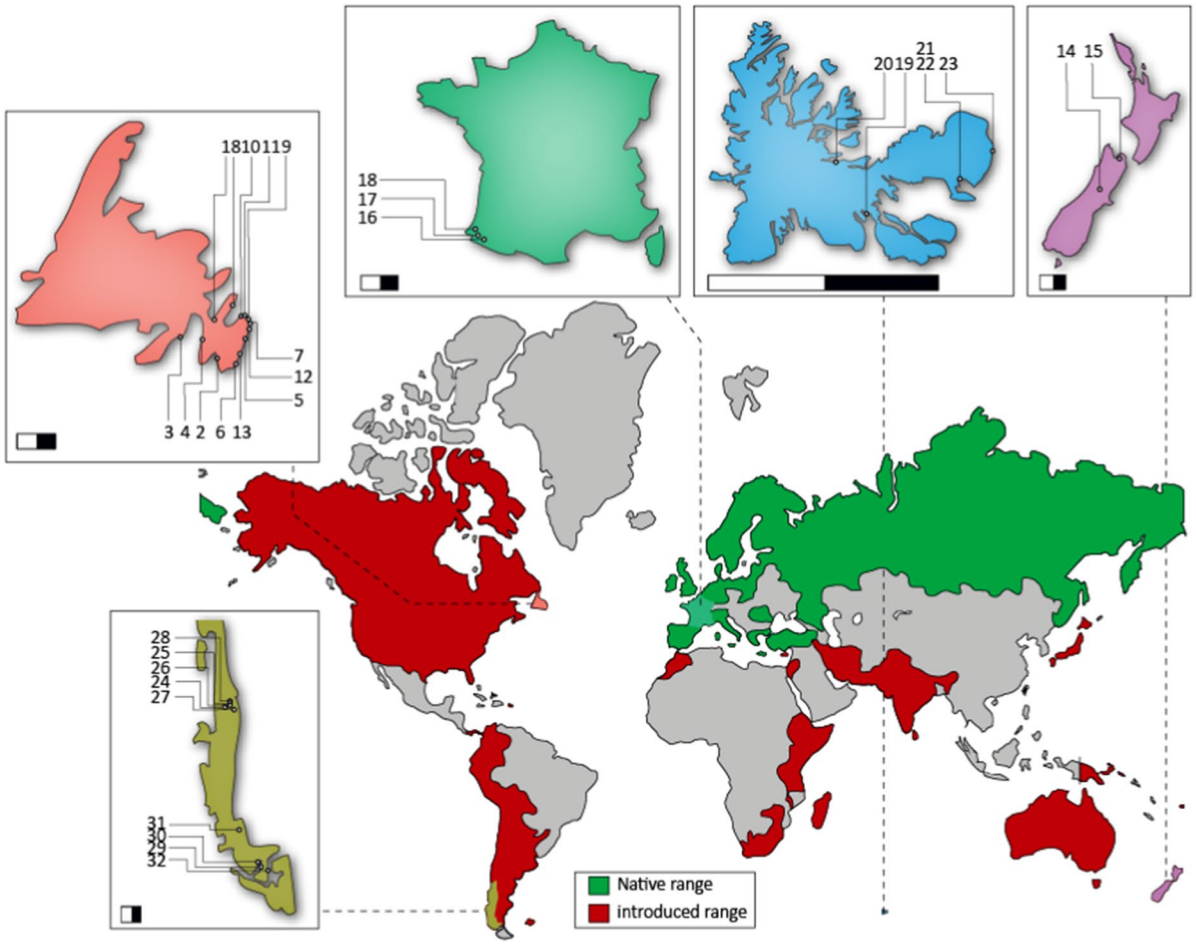

Fig. 1 Brown trout sampling locations. Sampling locations across the globe, with respect to native (green) and introduced (red) ranges (Data source: GISD 2022). Numbers refer to population identification as reported in the supplementary file 1. The black and white bar in each submap indicates a 100 km distance. Please note this map does not indicate country wide presence, but merely that the species is categorized as native/alien within that country

(Kinnison et al. 2003). For brown trout specifically, body shape differs markedly among populations and frequently correlates with habitat characteristics, suggesting adaptive responses to environmental challenges (Drinan et al. 2012; Pakkasmaa and Piironen 2000; Westley et al. 2012).

While previous work on morphological variation of different fish species has emphasized variation *among* populations (Oke et al. 2017; Riesch et al. 2020), our interest is centered on variation *within* populations that is most immediately relevant when considering responses to environmental change. Here, we investigated body shape variation of brown trout from various populations originating from all around the world, including the native range and remote introduced locations exhibiting contrasted founding population size (number of brown trout introduced to an area) and time since founding (number of years between the introduction and our sampling). Our analysis, therefore, aims at investigating whether the amount of morphological variation follows detectable and comparable pathways in the various invaded regions of the globe, relative to the native range. More specifically, we quantified both the magnitude and co-variation (i.e. "integration" as defined as the interdependence between two or more traits due to shared developmental pathways or function, Klingenberg 2008) of inter-individual

differences within populations. We also tested the relationship between those measures of morphological variation and two factors of interest: founding population size and the time since founding. Standard expectations from the literature assume that brown trout in regions with fewer founders would traditionally exhibit lower inter-individual variation compared to the native range. Predictions regarding co-variation (integration) of inter-individual differences are more challenging. Resulting from the differential elimination of pleiotropic variations between functional body parts, combined with the maintenance of pleiotropic effects within each body part, phenotypic (co) variance structures evolve to match patterns of local developmental and functional integration (Larouche et al. 2015, 2018; Orkney et al. 2021). We therefore expect integration to progressively increase through colonization-time under directional evolution imposed by strong local biomechanical constraints on body shape in response to local ecological/functional demands (Assis et al. 2016) and/or changes in their genetic covariance structure (Colautti and Lau 2015). This may be reinforced given the negative correlation classically observed across taxa between the magnitude of shape variation and the related level of co-variation.

Materials and methods

Locations and fish collection

Authors obtained (authors' records) lateral-view photographs of fresh adult or sub-adult brown trout originating from 32 rivers and lakes (hereafter treated as separate "populations") and covering five different "regions" in the world (Fig. 1a). These regions included the native range (France, 3 populations) and four remote introduced locations (Newfoundland, 13 populations; Kerguelen, 5 populations; Chile, 9 populations; New Zealand, 2 populations), ranging in dates of introductions from 1867 to 1993, with founding population sizes varying from a few individuals to 80.000 (all detailed information are accessible per population in Supplementary File 1). These populations are to our knowledge the only established populations for which photographs, as well as at least some information regarding dates of introduction and founder population sizes are all available. Founding dates and founding size were retrieved from existing publications and experts' opinions (information about possible admixture and supplemental stocking over time are also mentioned, see Supplementary File 1). We first screened all photographs to identify and exclude substandard images, such as those with the fish in a crooked position, with a tilted head, or showing optical distortion. We ultimately selected a total of 1891 images (mean number of 59 ± 93 individuals per population, encompassing sharp contrast in sample size among populations, ranging from 6 to 419 individuals, see Supplementary File 1).

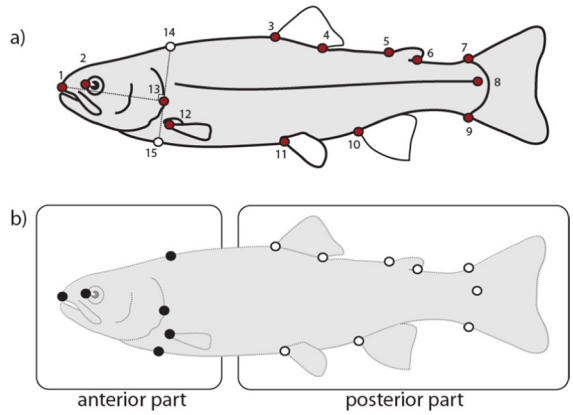

Fig. 2 Brown trout morphology. **a** Position of the 13 landmarks (red dots) and 2 semi-landmarks (white dots) placed on the photographs of each fish, and **b** partition of those landmarks in two functional modules (black for the anterior module and white for the posterior module)

Trout morphology

For all selected images, we used landmark-based geometric morphometrics to quantify body shape based on 13 landmarks and two additional slidings "semi-landmarks" (Fig. 2, Supplementary File 2). These landmarks were positioned to capture variation in functionally significant features related to feeding and locomotion. As is typical in geometric morphometric analyses of fish (Valentin et al. 2008), some images were influenced by non-informative "bending" that resulted from variation in fish placement during photography. Hence, a quadratic curve was fit through landmarks 1, 13, and 8 (Fig. 2, Supplementary File 2) and the entire configuration was 'unbent' so that the estimated quadratic curve became a horizontal straight line (Valentin et al. 2008). This procedure

was performed using routines from tpsUtil version 1.70 (Rohlf 2015). All landmark and sliding semi-landmark coordinates from the whole dataset were then superimposed using a single generalized least square Procrustes superimposition in tpsRelw version 1.45. Optimal semi-landmark superimposition was computed by minimizing bending energy of the deformation between the target shape and the reference (mean) shape (Green 1996; Bookstein 1997). Partial warp scores including both uniform and non-uniform components were calculated and used as descriptors of variation in body shape (Bookstein 1992). Some variation in partial warps can be due to allometry and, indeed, individual body sizes varied substantially within and among populations (Supplementary File 3). However, multivariate regressions of partial warp scores on log-transformed fish sizes explained only 1.17% of the variance. Thus, all further analyses directly used partial warp scores—without allometric adjustment—as obtained from the generalized least square Procrustes superimposition. Principal component analysis (PCA) of the partial warps and uniform components was performed using tpsRelw version 1.45 (Rohlf 2015).

Data are available from the institutional *dataPartage* Digital Repository: https://doi.org/10.15454/WAJNGA.

Here, we aim at quantifying both the magnitude and co-variation of inter-individual differences within populations. For this purpose, we consider three aspects of morphological variation at the *within* population level: (i) shape variation (*SV*) quantifies the magnitude of inter-individuals differences in a sample (Foote 1993), (ii) overall body integration (*OBI*) quantifies the degree of co-variation among individuals (i.e. the congruence of within-individual variations between individuals, Olson and Miller 1958; Pavlicev et al. 2009), and (iii) functional integration (*FI*) refines OBI by targeting co-variation between different "modules" of interest (here, anterior and posterior body parts) (Adams 2016; Escoufier 1973). These three measures thus cover both basic and multidimensional morphological variation.

Shape variation (*SV*)

Shape variation (i.e. the magnitude of inter-individual morphological differences) can be estimated and compared with a variety of metrics (Roy and Foote 1997; Ciampaglio et al. 2001). Foote's overall morphological disparity (Foote 1993) is one of the most widely used:

$$SV = \frac{\sum_{j=1}^{N} d_j^2}{N-1}$$

where d_j is the distance of individual shape *j* from the population's centroid (the population mean calculated over the *N* shapes). *SV* is thus the mean squared distance of individual shapes from the average population's shape and is therefore sample-size independent. *SV* was computed with the DisparityBox v8 from the IMP package (Sheets 2003) and a bootstrap procedure (2500 randomizations) was used to obtain its 95% confidence interval. This procedure takes into account uncertainty in the computation of the mean shape in the hyperspherical morphospace (Zelditch et al. 2003).

Overall body integration (*OBI*)

Integration is a measure of how phenotypic variation reflects multiple body parts that are correlated with each other (Olson and Miller 1958; Armbruster et al. 2014) due to shared developmental pathways or functions (Klingenberg 2008). It is related to co-variation among individuals. This co-variation in body shape can be quantified as the distribution of eigenvalues in PCA (Klingenberg 2008). If the variance among eigenvalues is high, then shape variation is concentrated in just a few dimensions (directions) of shape space. If the variance among eigenvalues is low, then shape variation is distributed more evenly across multiple dimensions (directions). We therefore examined the percentage of variance explained by the first two PCA axes as a simple measure of overall body integration (Pavlicev et al. 2009). Alternative considerations based on either the first three axes, or based on only axes 2 and 3, did not change our conclusions (results not shown). Given our interest in the deviations of individuals from their respective group means (i.e., within-population variance), rather than the overall grand mean, separate PCAs were computed for each population.

Contrary to *SV*, the percentage of variance explained by the first two PCA axes could be influenced by sample size (Pavlicev et al. 2009)—and

sample size varied dramatically among our populations. We corrected this potential bias using a simple bootstrap procedure (illustrated in Supplementary File 4). Specifically, all individuals, irrespective of their population, were resampled with replacements to create datasets of increasing size, ranging from 6 to 419 individuals (5000 iterations per sample size). For each dataset, a PCA was computed and the associated percentage of variance explained by the first two PCA axes was recorded. For each sample size, we therefore obtained the null distribution of the mean (±s.d.) expected percentage of explained variance for randomly chosen individuals. Relative deviations of each population from the null distribution (i.e., original value minus mean expected value, divided by its standard deviation) were therefore used as the measure of overall body integration. Positive values thus indicate stronger overall body integration than expected based on randomly chosen individuals, whereas negative values indicate weaker overall body integration than expected based on randomly chosen individuals. In other words, higher values correspond to a strong congruence of body shape variation between individuals, while lower values indicate that shape variation exhibit more singular individual patterns.

Functional integration (*FI*)

The above-described overall body integration (*OBI*) is an omnibus approach to integration (i.e., it considers all traits equally), and so we also evaluated a functional version of morphological integration. In this case, we quantified the degree of covariation between anterior and posterior modules (i.e., bipartite modularity). We therefore subdivided the landmarks into the two corresponding modules (Fig. 2b). The anterior and posterior body parts of fishes are candidates for functional modules/units because they are tightly related to feeding (anterior) and swimming (posterior) respectively (Langerhans 2008). Apart from functional considerations, such an anterior–posterior division has a developmental basis given that differences along this axis appears early during larval development (Kimelman and Martin 2012). The degree of integration between antero-posterior modules was quantified using the covariance ratio, a sample-size independent ratio of the covariation between modules relative to the covariation within them (Adams 2016). The covariance ratio varies from zero to positive values, with the latter indicating increasing degrees of covariation between modules and, hence, higher integration between the modules (Adams 2016). In other words, higher *FI* indicates similar antero-posterior variation among individuals.

To test for the relevance of this bipartite modularity, a randomization test for the whole dataset was computed by comparing the empirical value to the value expected under the null hypothesis of random assignment of variables to partitions, 10 000 iterations within Geomorph R package, (Adams and Otárola-Castillo 2013). We then computed the *FI* (measured using the covariance ratio) between antero-posterior modules for each population separately based on the within-population covariance matrix extracted from the initial Procrustes superimposition, and compared the obtained values with the overall body integration index. This latter comparison allowed us to investigate whether overall body integration relied on different degrees of concerted shape co-variation between anterior and posterior body parts. *FI* was computed using the *Geomorph* R package and a bootstrap procedure (10 000 randomizations) was used to obtain its 95% confidence interval.

Correlation between morphological measures and comparison between native and introduced ranges.

Because all three measures (*SV*, *OBI*, *FI*) are derived from the same initial dataset, we assessed the correlation between each pair of measures (using Spearman correlation coefficient), so to quantify possible constraints between them. For instance, *SV* might be strongly and negatively correlated to *OBI* and *FI*, indicating that a modular organization will facilitate the increase in morphological variance. Or, *OBI* and *FI* could be very correlated, which would indicate that most of the integration is actually captured along the antero-posterior axis. In addition, we performed Mann–Whitney tests (two-tailed test) to compare morphological measures between native and introduced ranges.

Effects of founding population size and time since founding

Founding population sizes and times were sometimes precisely known and other times had to be estimated

from information in the literature and reports (see Supplementary File 1). We therefore created a pseudo-quantitative variable, using a logarithmic approach (base 10) to mainly account for major differences in founding population sizes and to buffer the impact of uncertainty to some extent. This led to a simple quantitative variable F ranging between 1 and 4 (with F = 1 for n < 10, F = 2 for 10 < n < 100, F = 3 for 100 < n < 1000, and F = 4 for 1000 < n, with n being the expected number of propagules that founded a given population). For each population, time since founding was measured as the number of years between sampling and the date of founding as reported in the supplementary file 1. To test the fixed effects of founding population size (F), time since founding (T), and their interaction on morphological variables we constructed linear models where $Y_{i,j}$ indicates population i for region j and Y stands for *SV*, *OBI*, or *FI*). The full models were written as:

$$Y_{i,j} = \alpha * T_i + \beta * F_i + \gamma * T_l * F_i + \varepsilon_i,$$

With α, β, γ, being the linear model parameters to estimate for the effects of F, T, and their interaction respectively, and ε_i being normally distributed residuals. For each morphological variable (*SV*, *OBI*, *FI*), we used a stepwise comparisons approach based on Akaike Information Criterion (AIC) to select the best model starting from the full model given above.

These analyses treated populations as the unit of replication, which is conceptually appropriate. However, it might also be argued that the different populations within a region are not independent, and—indeed—our estimates of founding population size and time since founding were sometimes identical for multiple populations in a region. The reason was that, sometimes, information was available for the introduction to an area but not for each specific population we sampled in that region. To ensure that this non-independence did not impact our overall conclusions, we also ran a linear mixed effect model wherein the regional effect was modelled as a random variable (See Supplementary File 7). Please, note that such an alternative analysis does not change the main conclusions of the current study.

Results

The different measures of morphological variation (*SV*, *OBI*, *FI*) captured different aspects of shape variation as revealed by low to moderate correlations (Supplementary File 5). For instance, the estimates of *SV* and *OBI* were not correlated among populations (Spearman $\rho = -0.28$, $p = 0.119$, Supplementary File 5a); nor were *SV* and *FI* (Spearman $\rho = -0.15$, $p = 0.398$, Supplementary File 5c). Estimates of *OBI* and *FI* were moderately and positively correlated (Spearman $\rho = 0.54$, $p < 0.001$), yet they differed substantially in some instances (Supplementary File 5b). In Kerguelen, for example, *OBI* varied dramatically among populations whereas *FI* was relatively constant. In Chile, by contrast, *FI* varied dramatically among populations whereas *OBI* did not. Canadian populations exhibited an intermediate pattern, with variable levels of either OBI or FI among populations. The three measures of variation thus provide complementary insights into phenotypic variation in invasive populations that can be investigated separately (Fig. 3). Since populations with limited sample sizes did not differ even qualitatively from the other populations within each region, they were all fully considered as replicates of the same parameter within those regions.

Shape variation

Shape variation (*SV*) was measured as the total variation among individuals in morphological space within each population (equal to the mean squared distance among forms). The mean (± SD) *SV* value was 0.00082 (± 0.00035). The highest *SV*s were recorded for some populations in Chile (min–max [0.00068–0.00202]) and Kerguelen (min–max [0.00079–0.00148]), followed by Canada (min–max [0.00047–0.00076]) and New Zealand (min–max [0.00075–0.00089]), (Fig. 3a). Populations in the native range had the lowest *SV*s (min–max [0.00057–0.00070], with a mean value of 0.00063 ± 0.00006 among French populations, compared to 0.00084 ± 0.00037 among all other populations). Native and introduced ranges did not exhibit significantly different magnitude of shape variation (Mann–Whitney test, W = 59, p-value = 0.34). Overall, the key conclusion was that total shape variation for invasive populations—even those founded by

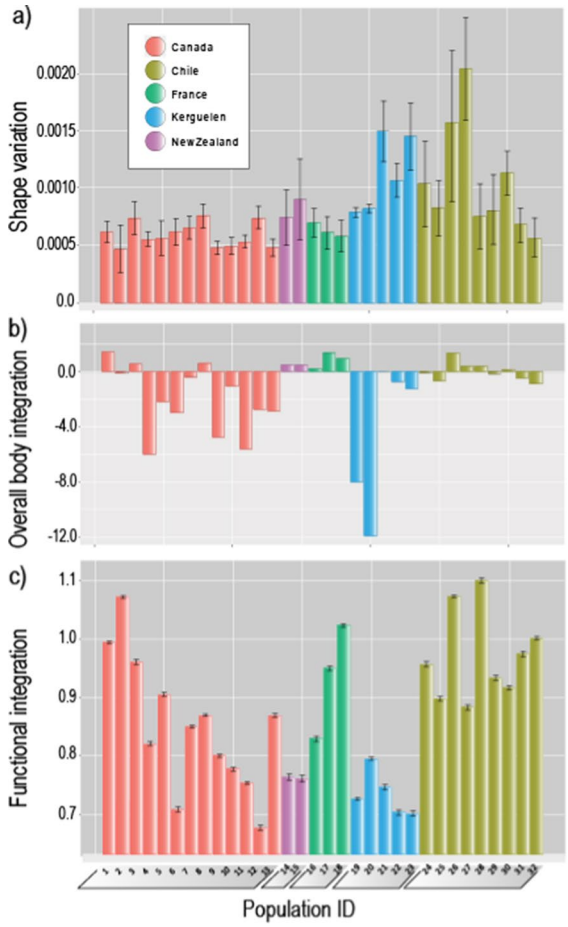

Fig. 3 Indicators of morphological variation in brown trout per population classified by regions. **a** Shape variation (expressed using Foote's disparity index) and its 95% bootstrapped confidence interval (2 500 randomizations) for all rivers. **b** Overall Body Integration accounting to sample size (using the percentage of variance explained by the first two PCA axes and calculated as the relative distance to the mean expected value, using a bootstrap approach). Negative values indicate reduced integration relative to global random expectations. **c** Functional Integration, and its bootstrapped 95% confidence interval (10 000 randomizations), measured as the degree of covariation between anterior and posterior modules, relatively to covariation to other modules. Regions and populations were arbitrarily organized following population identification as reported in the supplementary file 1

only a handful of introduced fish (e.g., Kerguelen)—is not lower than total shape variation for native populations.

Overall body integration

Overall body integration (*OBI*) represents the extent to which morphological variation is channeled in just a few dimensions as opposed to being spread across many dimensions of shape space, and is related to co-variation among individuals. *OBI* varied dramatically among populations (mean ± SD of -1.4 ± 2.9, min–max [− 11.9, 1.3]), (Fig. 3b). The lowest values relative to random expectations were generally seen in Kerguelen (mean ± SD of − 4.3 ± 5.2, min–max [− 11.9, − 0.01]) and Canada (mean ± SD of − 2.02 ± 2.42, min–max [− 6.0,1.3]), suggesting particularly low morphological integration in these regions (i.e. weak co-variation among individual). The highest *OBI* values relative to random expectations were seen in New Zealand (mean ± SD of 0.46 ± 0.01, min–max [0.45,0.47]) and France (mean ± SD of 0.83 ± 0.58, min–max [0.20,1.36]), indicating slightly higher than expected morphological integration in these regions (i.e. strong co-variation among individual). The key conclusion, then, is that overall body integration for invasive populations (mean value of − 1.63 ± 3.03 among invasive populations)—even those founded by only a handful of introduced fish—is statistically slightly different than overall body integration for native populations (mean value of 0.83 ± 0.58 among French populations, Mann–Whitney test, W = 11, p-value = 0.03).

Functional integration

Turning to a more functional view of integration (*FI*), we examined correlations between two functional/developmental modules (anterior versus posterior). These two body regions do indeed seem to be somewhat separate modules given that *FI* was generally lower than the random expectation (10 000 iterations, FI = 0.8655, p = 9.10–4, Supplementary File 6). *FI* differed rather markedly among populations (mean ± SD of 0.86 ± 0.12, min–max [0.67, 1.10], Fig. 3c). Canadian populations were particularly variable in *FI*: with some populations showing very high *FI* and others very low *FI* (mean ± SD of 0.85 ± 0.11, min–max [0.67, 1.07]). Kerguelen populations figured among the lowest values for *FI* (mean ± SD of 0.73 ± 0.03, min–max [0.69, 0.79]), indicating that, for these populations, modularity is extremely high between the anterior and posterior modules. Such

differences among populations were also observed in Chile although to a lesser extent, with a rather high average FI for this region (mean ± SD of 0.97 ± 0.07, min–max [0.88, 1.10]). Native populations from France showed intermediate FI values, with some clear differences between populations (mean ± SD of 0.93 ± 0.09, min–max [0.82, 1.02] among French populations, compared to 0.86 ± 0.12 [0.67, 1.10] among all other populations). Overall, native and introduced populations did not exhibit statistically different levels of functional integration (Mann–Whitney test, W = 27, p-value = 0.31).

Effects of population founding size and time since founding

When looking at the effect of founding population size and time since founding, we found contrasting results concerning the different morphological variables (based on model selection using AIC ranking, Table 1, see summary statistics in Supplementary File 8). Shape variation *SV* was not correlated with founding size or with time since founding. Overall body integration was influenced by both parameters in an interactive way ($R^2 = 0.40$, $p = 0.001$, $\gamma = -0.055 \pm 0.013$): in populations founded with a high number of propagules, OBI was higher in more recently founded populations, but when looking at populations founded with a small number of propagules, the opposite pattern was observed, wherein more recently founded populations had smaller *OBI* values (Fig. 4). It is likely, however, that this result is strongly influenced by two Kerguelen populations with extremely low *OBI* values and small numbers of founders (Supplementary File 1, Fig. 4). Finally, functional integration *FI* was not clearly related to either time since foundation or population founding size, since no model presented significantly lower AIC values than the others (Table 1). Note that including regions as a random factor on the intercept of the models produced similar results (Supplementary File 7)—with the exception of *OBI*, where only the founding size effect remained significant. Because some founding sizes were also uncertain for Chile (see Supplementary file 1), we also ran the model using lower values for this region (i.e., [100–1000[), but it did also not affect the general outcome of the model (data not shown). Regardless, it is clear that—no matter the model structure—population founding size and time since founding in introduced non-native populations do not strongly drive morphological variation and integration, possibly also explaining the lack of difference with native populations (Fig. 3).

Discussion

Classic expectations would suggest that populations founded by the introduction of a small subset of individuals from an ancestral population would have reduced genetic variation. Yet it is phenotypes—not genotypes—that interact with the environment and hence determine responses to new conditions and, ultimately, the success and spread of potential invaders. Besides emphasizing the large variation among populations, we overall report that invasive populations do not exhibit lower morphological variation than native populations at least for the body shape of brown trout from several remote areas of the globe. That is, variation in body shape was not lower for introduced populations than for native populations, even when those introduced populations derived from a very small number of founders irrespective of the time since founding. We also failed to detect increased morphological integration in older populations. We first discuss the basic patterns documented in our survey and then provide potential general explanations.

The distribution of variation and integration

On the one hand, genetically-reduced non-indigenous populations should exhibit reduced shape variance, as expected given the genetic/phenotypic correlation. On the other hand, when populations experience new environmental conditions, regulatory mechanisms involved in the expression of phenotypic variation can be challenged, resulting in increased phenotypic variance (Badyaev 2005; Hoffmann and Hercus 2000; Lazic et al. 2015). In particular, while acting on different levels, canalization (i.e. the ability to produce the same phenotype despite variation in genotype and environments among individuals) and developmental stability (i.e. the ability of a genotype to produce the same phenotype under the same environmental conditions by buffering individual's developmental noise) are two important developmental processes ultimately involved in determining the magnitude of

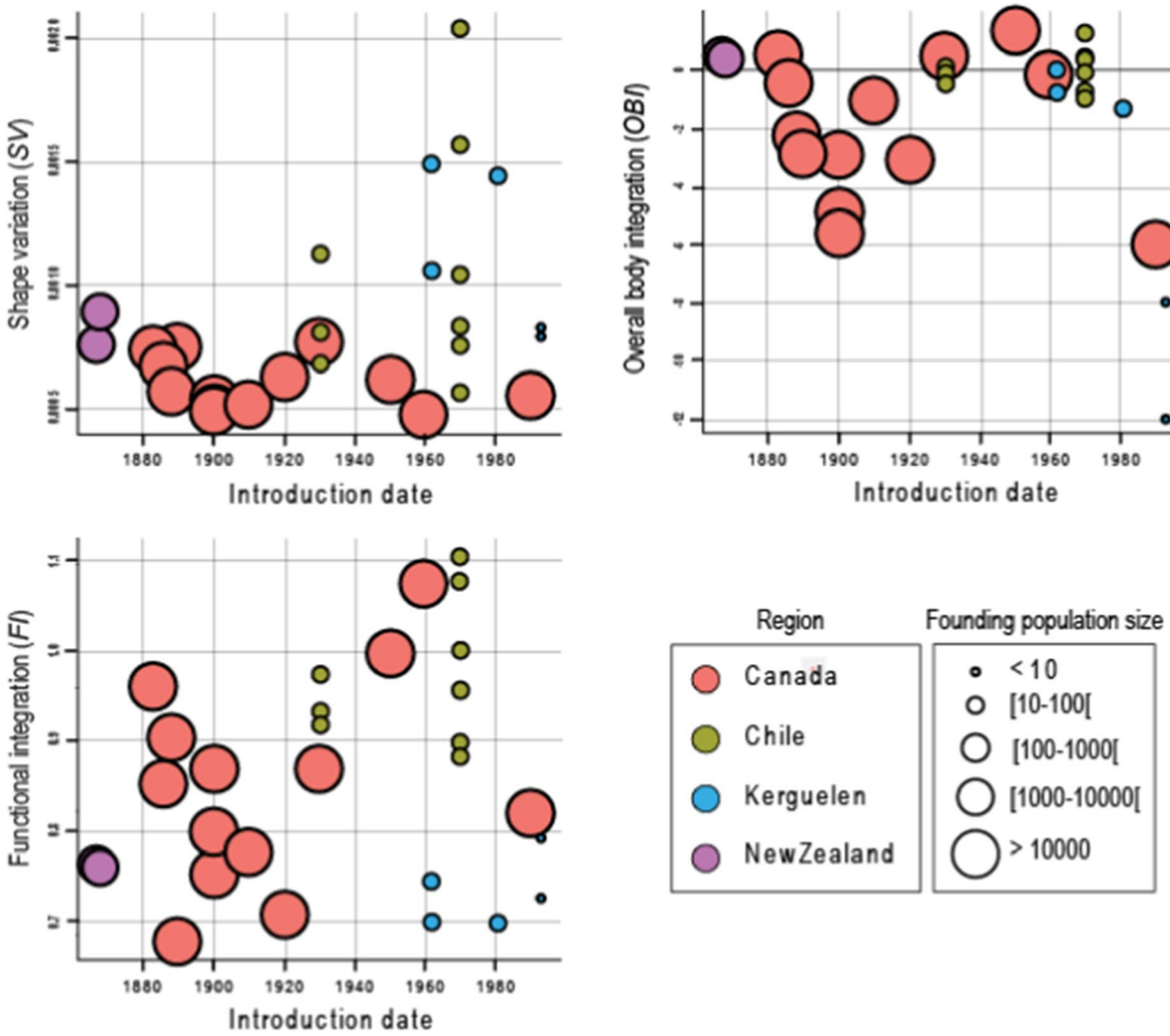

Fig. 4 Variation of shape variation (*SV*), overall body integration (*OBI*), and functional integration (*FI*) in the introduced ranges of the brown trout as a function of introduction date, founding population size and region

shape variation (Debat and David 2001; Hoffmann and Woods 2001; Scharloo 1991; Willmore et al. 2007). These two components are strongly affected by allometric growth (Klingenberg 2010) that is locally mediated by numerous environmental components. The extensive literature on environmentally-mediated change in allometry mainly rely on the idea that parts of the organism need to function together in a coordinated manner and that local developmental regulatory processes reduce maladaptive uncoordinated variation (Armbruster et al. 2014). Encountering new environmental conditions is therefore expected to reshape allometry passing through a transitorily relaxation of the canalization process (Lazic et al. 2015), that in turn increases shape variance. In addition, developmental relaxation may allow the expression of cryptic genetic variation, undetected under former conditions (Rutherford 2000). As such, we may expect shape variance to increase in non-native ranges, at least during the first stages of invasion (or the colonization front).

The two aforementioned theoretical frameworks (genetically and developmental processes) may lead to contradictory expectations concerning shape variance, with a reduced shape variance in genetically-reduced populations but an increased shape variance

Table 1 AIC values of the nested models for Shape variation (*SV*), overall body integration (*OBI*), and functional integration (*FI*) in the brown trout

Model	Shape variation (*SV*)	Overall body integration (*OBI*)	Functional integration (*FI*)
Null	**−413.9624**	163.7582	−41.27372
Time	−376.3639	149.9649	−35.2534
Size	−377.6238	147.4928	−37.49235
Time + Size	−376.8891	149.4487	−42.30015
Time × Size	−378.313	**135.4547**	−41.98818

Factors are Time (since foundation) and Size (founding population size). Values in bold indicate substantially lowest AIC values (i.e., distant from at least 2 points from the nearest value), pointing at the models presenting the better tradeoff between parsimony and fit to data

in novel environment. However, most of the predictions have been addressed in stressful situations (considered here as environmental conditions in which homeostasis may be disrupted, ultimately causing a decline in individual fitness), based on genetically non-restricted populations. Considering its invasive status, the non-indigenous brown trout is encountering not-so-stressful environmental contexts (or at least, not sharply-diminished fitness). Our specific invasive context (i.e. potentially non-stressful environment with limited genetic diversity) has received little scrutiny. Our findings clearly emphasize that introduced populations of brown trout do not show substantially low levels of phenotypic variation as quantified using shape variation (*SV*). Our sampling from the native range of brown trout was not extensive (only France) and these populations might have experienced declines in variation due to various and interacting anthropogenic pressures (pollution, connectivity, fishing). However, gene flow is much more likely to have occurred among French and other European populations, and they are thus less likely to have experienced bottlenecks anywhere near the extent that must have been the case in many introductions. It is therefore possible that in new environmental conditions, the reduced efficacy of developmental regulatory mechanisms counterbalances the effect of limited genetic diversity. In particular, local environmental factors, such as temperature or nutrition, can directly affect the allometric growth, that in turn acts as a highly canalized process and a strong integrating agent (Klingenberg 2010), thus locally affecting the magnitude of shape variation. Similarly, morphological integration in fishes can respond directly to environmental conditions through ontogeny (Fischer-Rousseau et al 2009; Peres-Neto and Magnan 2004).

Co-variated structures generally evolve to match patterns of local developmental and functional integration (Klingenberg 2008) with antero-posterior modularity being well known in fishes (Larouche et al. 2015, 2018). Here brown trout indeed exhibit significant antero-posterior functional integration that considerably changes within and between geographic regions. However, such antero-posterior modularity does not capture all functional, nor developmental constraints since partial congruence was observed between *OBI* and *FI*, emphasizing their complementary use in quantifying integration. In particular, *FI* was always low when *OBI* was low, whereas *FI* could range from high to low when *OBI* was high. The fact that high overall body integration does not *always* trigger high functional integration indicates that regulatory processes might rely on distinct pathways, or hint at different selective regimes among populations, in which some populations are under selection for antero-posterior modular divisions, whereas others are not. Regardless of these speculations, our main result is that introduced populations of brown trout may not consistently have lower or higher integration (overall or functional) than do native populations.

Numerous potential constraints on adaptive evolution have been proposed, including the correlation of body parts that are not congruent with the pattern of correlated changes favored by selection (Maynard Smith et al. 1985). In this context, modular organization has broadly facilitated morphological diversification in association with development, trophic and locomotor aspects (Wagner and Altenberg 1996; Lexer and Fay 2005; Klingenberg 2008; Ornelas-García et al. 2017), with shape variance being usually negatively related to integration patterns (e.g. Goswami and Polly 2010; Claverie and Wainwright 2014; Collar et al. 2014). In Actinopterygians, modular evolution has also favored ecological diversification, in spite of strong biomechanical constraints imposed on fish body shape, by generating shape variation with distinct body regions showing semi-independent evolutionary trajectories (Larouche et al. 2015, 2018). Our initial assumption concerning the negative correlation between shape variance and functional integration was partly influenced by available knowledge

of morphological diversification at macro-evolutionary scales (e.g. Gerber 2013; Goswani et al. 2014). However, this hypothesis has received little scrutiny at a microevolutionary scale. In the present study, we failed to find a correlation between shape variance and integration (*OBI* or *FI*). Expanding the above expectations to the micro-evolutionary scale may be difficult since many environmental factors (including competition) can affect both disparity and integration (e.g. Závorka et al. 2017). For instance, increased climatic variability is correlated to lower levels of integration and higher evolutionary rates in both canids and felids (Conith et al. 2018). It is very much possible that on a micro-evolutionary scale, introduction or movements to new environments in brown trout trigger the same mechanism, selecting for lower levels of integration.

In general, the present study did not aim at investigating morphospace occupation (i.e. possible phenotypic variations among populations) but rather focused at the within population scale, with specific emphasize on global patterns (founding population size, time since founding and invasive/native status) that would inevitably superimpose local environmental conditions that should be contrasted across the species' now-global range. In absence of cross/nested design nor balanced sampling strategy we did not formally investigate the effect of local putative confounding variables. However, our data emphasized the absence of global patterns, despite variations among populations. We therefore rather suspect that both biotic and abiotic local factors (not quantified in the present study) are more prone to affect trout morphology, causing local changes in the magnitude and covariance of phenotypic variations across and within geographical regions that should be addressed on a case-by-case basis. This complicates the straightforward paradigm in determining variational patterns in invasive populations. For instance, introduction to Canada—Newfoundland—involved some niche overlap with the native *Salvelinus* species. For New Zealand and Chile, native fish fauna probably facilitated the growth of introduced brown trout (Correa et al. 2012; McIntosh et al. 2010), whereas in Kerguelen, no previous fish fauna occupied the freshwater ecosystems. This variation in biotic interactions likely affected the initial niche breadth of brown trout (Levine and D'Antonio 1999), with different selective regimes promoting differences in shape variation and morphological integration (Hedrick et al. 2020) that could stabilize after several decades or a century (Závorka et al. 2018).

Founder effect and time since founding

To explain the variational patterns of body shape among the studied populations, we further hypothesized that founding population size could be a significant factor, where small founding size would be limiting phenotypic variation through allegedly reduced genetic variation. This was not the case: in fact, we even found slightly higher values of shape variation in populations founded by few individuals. This is for example clearly the case in some Kerguelen populations that exhibited the highest shape variation, with locations founded by the fewest number of individuals (e.g. populations 19 and 20 have been founded by 2 and 3 founders respectively, and displayed an average shape variation, population 21 was founded with 23 individuals, and displayed high shape variation). Similar results have been documented in other biological systems (Fowler and Whitlock 1999; Gozlan et al. 2020). Likewise, morphological integration (OBI or FI) was not—or weakly—correlated to founding population size, indicating that covariance between morphological traits cannot be simply predicted by expectations regarding inbreeding. Granted, our appraisal of founding population size was limited: in Chile for example, where imported batches ranged between 1000 and 10,000 individuals, it is likely that some rivers were actually stocked with lower numbers. Additionally, the lack of variation in founding size among some groups of populations like in Chile prevented us to draw definite conclusions.

Time since founding was then investigated, as a proxy for past selection that may have eroded phenotypic variation, or oriented it in new directions. Shape variation appeared to be completely independent of time since founding: the amount of raw morphological variation thus was not quantitatively affected by possible directional selection in these new environments, a rather surprising result considering what is generally expected (Drinan et al. 2012; Pakkasmaa and Piironen 2000; Westley et al. 2012)—but we discuss that seemingly counter-intuitive pattern below. Possibly even more surprising was the fact that morphological integration also appeared to be mostly unaffected by time since founding. This was the

case for either overall body integration or functional integration. Our initial assumption was that morphological integration could initially be reduced due to possible changes in the genetic covariance structure between traits, and then would increase under the effect of directional selection (Assis et al. 2016; Colautti and Lau 2015). It appears more likely that local or regional environmental characteristics may have led to differences in morphological integration, or that selection was not consistent over time to produce that expected pattern.

How can such high phenotypic variation be present despite extremely limited numbers of founding individuals?

One class of possibilities relates to the nature of genetic variation in the founding population. First, admixture resulting from multiple introductions can increase the diversity of newly founded populations (Roman and Darling 2007), sometimes exceeding the diversity observed in the initial distribution area (Correa and Moran 2017; Lavergne and Molofsky 2007). Similarly, supplemental stocking over time may also act as an additional source of genotypic/phenotypic variation. In the present case, the level of admixture for each population was only partially known, preventing a thorough analysis of this effect. In Chile, various origins of fish were used for introductions, with probable admixture in several sites and supplemental stocking over time in the southernmost localities, yet the outcome in terms of shape variation was highly variable among populations. Likewise, in New Zealand, many shipments occurred (McDowall 1990; Thomson 1922). In Kerguelen, some recently introduced populations only had 2 or 3 founders, and these populations still presented high shape variation, but their founders were taken in other previously colonized areas of the archipelago, where admixture may have occurred (Lecomte et al. 2013). Second, some studies have shown a flush of genetic and phenotypic variation immediately after a bottleneck as a result of "genetic reorganizations" that—for example—convert non-additive genetic variance to additive genetic variance (Cheverud and Routman 1995; van Heerwaarden et al. 2008). Third, several additional mechanisms can generate rapid increases in genetic variation after a founder event (Bernatchez 2016; Haanes et al. 2013; Kaeuffer et al. 2008; Labonne et al. 2016)—and these mechanisms will be considered below. Fourth, small population size is often related to an increased probability of inbreeding, but inbreeding itself can also sometimes lead to increased phenotypic variation (Fowler and Whitlock 1999).

Another class of possibilities relates to how environmental effects manifest as phenotypic plasticity (Badyaev 2009; Baldwin 1896; Crispo and Chapman 2010; Richards et al. 2006). Indeed, a recent meta-analysis of laboratory experiments in fishes has shown that experimentally increasing temperatures increases phenotypic variation (O'Dea et al. 2019). Such effects could arise in two general ways. First, diverse environmental influences across individuals introduced to new environments could increase the environmental contribution to phenotypic variation for a given level of genetic effects (i.e., the heritability will decrease, Hoffmann and Merilä, 1999; Lande 2015; Valiente et al. 2010). Second, genotype-by-environmental interactions can mean that exposure to new conditions, such as following introduction to a novel environment, can reveal "cryptic" genetic variation that was not evident in the ancestral environment (Gibson and Dworkin 2004; Paaby and Rockman 2014). The extent to which plasticity may be transgenerational (e.g. Salinas and Munch 2012) and shape the evolutionary trajectories in our findings is currently unknown.

It is also possible that the original founding events did, in fact, reduce phenotypic variation, but that variation has since recovered to "normal" levels (Selechnik et al. 2019). Indeed, empirical and theoretical studies tend to find such short-term decreases can—sometimes—rapidly disappear in only a few generations (Du et al. 2016; Willis and Orr 1993). In our analysis, time since introduction was not strongly correlated (if at all) with phenotypic variation. Yet it is also possible that phenotypic variation increased so quickly after the founding event that we did not capture its initial decline. Several of the above-described mechanisms increase phenotypic variation in just a few generations following a bottleneck, and other mechanisms can come into play on the time scale of our study. For instance, mutation can contribute to phenotypic variations over tens of generations (Nei 2007) and selection for heterozygosity and inbreeding avoidance can rapidly increase genetic variation on similar time scales (Talla et al. 2019a, b; Talla et al. 2019a, b). Indeed, we have evidence for both of these

latter mechanisms being important in the Kerguelen Island brown trout populations that were founded by so few individuals and yet have such high phenotypic (and genetic) variation (Labonne et al. 2016, 2020).

Soft landings

An important contributor to our results might be the relaxed selection on introduced brown trout due to "enemy release" (Colautti et al. 2004). That is, introduced brown trout often experienced reduced competition, escape from predators and pathogens, and often naïve prey bases. Conditions such as these provide a "soft landing": selection on specific phenotypes might have been relaxed—hence allowing persistence of initially maladaptive phenotypes and allowing the rapid expansion of phenotypic variation (Brady et al. 2019). The fact that phenotypic integration does not seem to increase as time since founding increases may be due to initial maladaptation that shaped the within-population covariance structure among traits. In any case, this high (and possibly maladapted) variation then might facilitate rapid ongoing adaptation to other new environments. Indeed, a number of studies show that introduced fishes, including brown trout, show rapid population divergence in seemingly adaptive directions. Indeed, examples of such divergence come from our study populations in Canada (Westley et al. 2012), Kerguelen (Aulus-Giacosa et al. 2021; Marandel et al. 2018), New Zealand (Kinnison et al. 2003) although less so in Chile for the moment (Monzón-Argüello et al. 2014). Disentangling this sequence of effects will require further work, especially controlled experiments. One such experiment was unable to demonstrate the rapid building of local adaptation of Brown trout in Kerguelen islands (Labonne et al. 2020). Given that brown trout now occupy nearly all suitable habitats globally (Lobón-Cerviá and Sanz 2017; McIntosh 2011), and that introduction to new locations would be unethical, exploring these options will likely involve other study species.

In conclusion, the dynamics of phenotypic variation and subsequent phenotypic integration in this study were not obviously structured by founding population size or time since founding. Thus, it appears that the general expectations associated with the small population paradigm do not apply universally. We suggest that this outcome reflects the many processes that can increase variation after introduction to a new environment and also the many uncontrolled factors that vary among introduced habitats: ecological contrast, competition, and niche availability. Our comparative analyses of brown trout shape at a microevolutionary scale suggest a more complex suite of processes driving and linking shape variation, body integration, and functional integration. An overall conclusion is that no common trends were associated with the various introduced ranges examined, and time trends will not be easily forecastable.

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Declarations

Conflict of interest The work is all original research carried out by the authors.

Consent to participate All authors agree with the contents of the manuscript and its submission to the journal.

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