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Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr

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Summary

1. A phenotypic syndrome refers to complex patterns of integration among functionally related traits in an organism that defines how the organism interacts with its environment and sustains itself.
2. Human-induced biological invasions have become important sources of environmental modifications. However, the extent to which invasive species affect the phenotypic syndromes of individuals in a native is currently unknown. Such knowledge has important implications for understanding ecological interactions and the management of biological invasions.
3. Here, field monitoring in a natural stream were combined with standardized estimates of behavioral, physiological and morphological traits to address the hypothesis that coexistence with a non-native invader induces a novel environmental pressure that disrupts the adaptive integration among phenotypic traits of the native species. We compared the strength of integration among key phenotypic traits (i.e. aerobic scope, standard metabolic rate, body growth, activity, and body shape) and ecological niche traits (i.e. spring and summer diet, home range size, daily movements) of an allopatric group of native brown trout (*Salmo trutta*) with a group of brown trout living in sympatry with non-native brook trout (*Salvelinus fontinalis*).
4. We found that the integration of phenotypic traits was substantially reduced in the sympatric brown trout and that allopatric and sympatric brown trout differed in key phenotypic and ecological niche traits. Brown trout living in sympatry with non-native brook trout consumed more terrestrial prey, had smaller home ranges, and a stouter body shape. Sympatric brown trout also had lower specific growth rate, suggesting a lower fitness.
5. The results are generally in line with our hypothesis suggesting that the reduction in fitness observed in sympatric brown trout is caused by the breakdown of their adaptive phenotypic syndrome. This may be caused by differences in the plasticity of the response of phenotypic traits to the novel selection pressure induced by the non-native species. Our results may help explaining deleterious effects of non-native species reported in the absence of direct competition with the native species.

Key-words: biological invasions, diet, metabolic rate, morphology, pace-of-life syndrome, personality, Salmonidae

Introduction

The rapid environmental changes in ecosystems worldwide as a result of human activity represent substantial challenges (Hillerislambers *et al.* 2013), as organisms are required to adjust multiple phenotypic traits to maintain fitness under novel environmental pressures (Lande & Arnold 1983; Pigliucci 2005). Biological invasions are major human-induced environmental changes, causing intense selection and rapid adaptation in various organisms (Colautti & Lau 2015). The impacts of non-native invasive species can affect all levels of biological organization, ranging from genes to whole ecosystems (Cucherousset & Olden 2011; Buoro, Cucherousset & Olden 2016). Coexistence with a non-native species has been shown to induce changes in behavior (Blanchet *et al.* 2008),

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morphology (Langkilde 2009), and life-history traits (Leyse, Lawler & Strange 2004; Öhlund *et al.* 2008) of native species. However, studies focusing on the impact of non-native species have generally estimated the phenotypic trait responses of native species independently (e.g. Leyse, Lawler & Strange 2004; Blanchet *et al.* 2008; Langkilde 2009), but have not considered changes in their integration. Such knowledge may improve the understanding of ecological interactions and the management of biological invasions.

Phenotypic integration (Pigliucci 2003; Murren 2012), character coherence (Clausen & Hiesey 1960), or phenotypic syndrome (Pigliucci & Hayden 2001) are terms referring to patterns of covariation among functionally related traits that defines how an organism interacts with its environment and sustains itself. A specific hypothetical example of such a phenotypic syndrome is the pace-of-life syndrome (Réale *et al.* 2010), which integrates physiological, behavioral, and life-history traits along a continuum of slow-fast production rate. Correlations among phenotypic traits across individuals in a population can be constrained by gene interactions (Lande & Arnold 1983; Pruitt *et al.* 2010) and by selection trade-offs resulting from current environmental pressures (Bell & Sih 2007; Dingemanse *et al.* 2007; Nicolaus *et al.* 2016). Integration of traits into a phenotypic syndrome can thus maintain consistent inter-individual differences, even in traits that are expected to be relatively plastic such as foraging or movement strategies (i.e. ecological niche) (Wilson & McLaughlin 2007; Závorka *et al.* 2015).

The potential impact of invasion on the phenotypic syndrome of a native species can be illustrated by a population containing individuals that vary in territoriality (Jenkins 1969). Territorial individuals as opposed to non-territorial ones are often highly active and aggressive, have high metabolic rates, and maintain a stable position within the habitat patch they defend (e.g. great tit, *Parus major*: Dingemanse & de Goede 2004; European catfish, *Silurus glanis*: Slavík, Horký & Závorka 2014). Non-native invaders can induce an additional competitive pressure (Fausch & White 1981; Cole & Harris 2011) and reduce the predictability of resource distribution (Carpenter *et al.* 2011), which may decrease territory value and eventually disrupt the adaptive integration among phenotypic traits (e.g. territory size, activity, metabolic rate, growth). Therefore, one might hypothesize that the novel selection pressures induced by the non-native species breaks down the association among phenotypic traits in the native species, at least until a new equilibrium is established (i.e. lag-time: Dewitt, Sih & Wilson 1998; Fischer, Ghalambor & Hoke 2016). In addition, if the original phenotypic syndrome has an adaptive value, its breakdown should be associated with a decrease in individual fitness (Réale *et al.* 2010).

In this study, we investigated the strength of integration among five phenotypic traits [i.e. specific growth rate (SGR), body shape, standard metabolic rate (SMR), aerobic scope (AS), and activity] and three ecological niche traits [i.e. home range size (HR size), daily movement, and diet composition in spring and summer] in a territorial native species, brown trout (*Salmo trutta*) living in allopatry or in sympatry with another territorial species, non-native brook trout (*Salvelinus fontinalis*). Brook trout are known to have negative effects on the growth, survival and reproduction of brown trout in European streams (Öhlund *et al.* 2008). However, the mechanisms underlying these effects are not well understood, as the ecological niches of these species have previously been found to be largely segregated (Blanchet *et al.* 2007; Korsu *et al.* 2012). In addition, brown trout tends to dominate brook trout in direct interactions (Fausch & White 1981; Blanchet *et al.* 2007).

Based on the hypotheses discussed above, we predicted that the association of phenotypic traits in brown trout would be weaker in the sympatric than in the allopatric scenario, and that the breakdown of the phenotypic syndrome would be associated with reduced growth rate, which we assume to be a proxy of fitness (Roff 1992).

Materials and methods

STUDY SITE AND FISH SAMPLING

The study was conducted during the spring and early summer of 2015 within the upstream stretch of Ringsbäcken, a small stream running through a sub-boreal forest in southern Sweden (57°40·318′N, 12°59·300′E; see Appendix S1, Supporting Information). The earliest electrofishing record indicating the presence of a self-reproducing population of brook trout in Ringsbäcken dates back to 1985 (Sers 2013).

Brown and brook trout were collected by electrofishing (LR-20 B; Smith-Root, Vancouver, WA, USA) within four 250 m long sampling sites (Fig. 1) between 7 and 10 April 2015. Sampling site 4 represented the allopatric group of brown trout, while individuals from sampling sites 1, 2, and 3 were sympatric with an increasing proportion of brook trout (see Fig. 1 and Appendix S1). Each captured individual was anaesthetized (benzocaine; 0·5 mL L^{-1}), measured for fork length and body mass, and tagged with 12-mm PIT-tags (HDX ISO 11784/11785; Oregon RFID, Portland, OR, USA) implanted into the body cavity. Fish were subsequently placed on their left lateral side and photographed with a digital camera (Canon PowerShot G16; Canon Inc., Tokyo, Japan, see Appendix S2). A small clip of the pelvic fin (0·5 cm^2) was taken and stored on ice for stable isotope analysis. Individuals were allowed to recover before being released back into the stream within 50 m of their capture location. Age-1 trout, determined via the examination of scales, were the focal group for the experiment and therefore the maximum body length for the experimental individuals was 110 mm. In total, 151 age-1 brown trout (body length mean ± SD: 83·68 ± 16·90 mm) and 70 age-1 brook trout (body length mean ± SD: 86·73 ± 9·93 mm) were collected and sampled.

MOVEMENT AND GROWTH RATE IN THE NATAL STREAM

We used two portable RFID antennas (Oregon RFID) to track the position of tagged individuals within the stream. Seven tracking surveys were conducted at 2-week intervals between 15 April and 1 June 2015. The stream was scanned in an upstream direction and the total length of the tracking stretch was 5500 m. However, the whole length of the tracking stretch was not scanned during all surveys due to logistical constrains (Fig. 1). During each tracking survey, observers were equipped with a GPS (eTrex 30 Garmin,

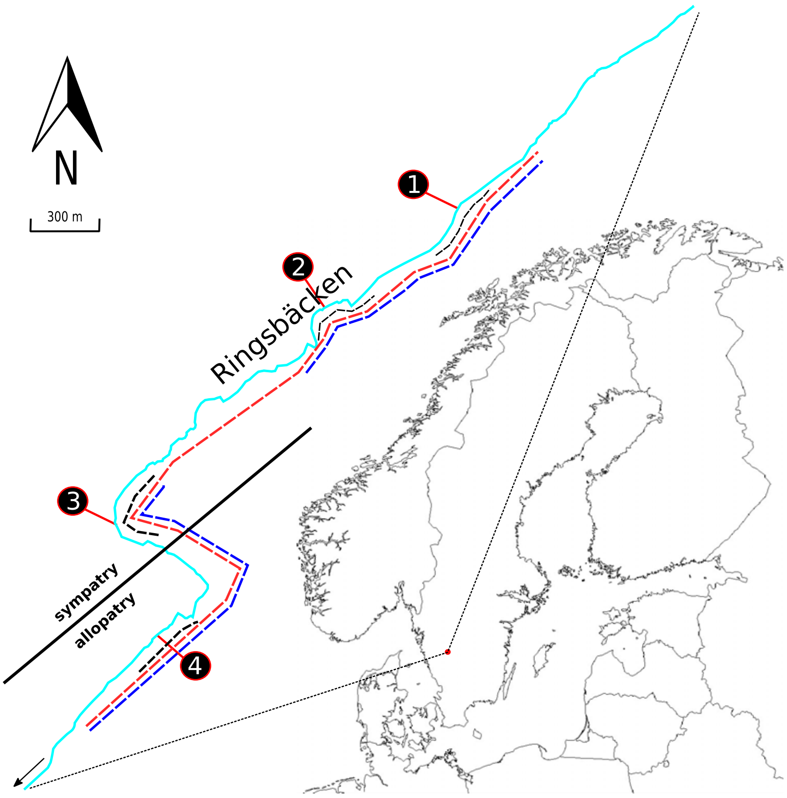


Fig. 1. Map of the study area displaying the four sampling sites. The sympatric groups of brown trout were located at sampling sites 1–3, whereas the allopatric group of brown trout was located at sampling site 4. Dashed lines along the stream display the length and position of the tracking surveys (black: a survey on 15 April 2015; blue: surveys on 24 April and 1 June 2015; red: surveys on 5, 14, 15, and 22 May 2015). (Alternative for a printed grayscale version – black: a survey on April 15, 2015; dark gray: surveys on 24 April and 1 June 2015; light gray: surveys on 5, 14, 15, and 22 May 2015).

Olathe, KA, USA) that automatically saved their positions every 6 s. Position of fish in the stream was then estimated by synchronizing time-stamps from the GPS with the RFID data logs. The precision of the positioning was checked at fixed reference points situated at the start, middle and end of the tracking stretch. The precision of positioning was ±2·4 m. Home range (HR) size for each individual was calculated as the interquartile distance between the positions of each individual detected from 15 April to 1 June 2015 (Höjesjö *et al.* 2007). Daily movement was calculated as the distance between an individual's position recorded during tracking surveys on 14 and 15 May 2015. Daily movement thus corresponds to the shift of an individual's position within 24 h and represents a short-term movement strategy in contrast to HR size, which summarizes the movements over the whole study period.

The final electrofishing was performed during 2 days on 3 and 10 June 2015. To increase efficiency of recaptures, we combined electrofishing with positioning of individuals, using the portable RFID antennas (Závorka *et al.* 2015). In total, 83 brown trout were recaptured (body length mean ± SD: 93·96 ± 18·42 mm) and transported to the University of Gothenburg, Sweden. In the laboratory, each recaptured individual was anesthetized (benzocaine; 0·5 mL L^{-1}), measured for fork length and body mass, and fin clipped for subsequent stable isotope analysis. Increment of body mass and length in grams and millimetres, respectively (*M*) of focal individuals during the time in days between tagging and recapture (*t*) was used to calculate SGR according to the following formula:

$$\mathrm{SGR} = \frac{\ln M_{\mathrm{final}} - \ln M_{\mathrm{initial}}}{t} \cdot 100$$

DIET COMPOSITION IN SPRING AND EARLY SUMMER

We used stable isotope analyses to estimate diet composition of the focal fishes. Fin samples and kick sampling of potential prey were collected at each sampling site in April and June, 2015. Putative prey was categorized into five trophic groups: aquatic grazers, aquatic predators, aquatic detritivores, terrestrial herbivores, and terrestrial predators. All samples (prey and fin clips) were oven dried (60 °C for 48 h) and ground into a homogeneous powder, using a mixer mill (Retsch MM 200, Haan, Germany). Isotopic analyses were performed at Cornell University Stable Isotope Laboratory (Ithaca, NY, USA). A Bayesian mixing model (SIAR, Parnell *et al.* 2010) was then used to quantify the relative dietary contribution (%) of each prey type to consumers (Layman *et al.* 2012). SIAR allows the integration of variability in prey and consumer stable isotope values and trophic enrichment factors. As the C : N ratio of invertebrates in the prey sample was high, their stable isotope values were mathematically corrected for lipid content following methods described in Post *et al.* (2007). Enrichment factors used for brook trout (+3·3 ± 1‰ for $\Delta\delta^{13}$C and +3·8 ± 1‰ for $\Delta\delta^{15}$N) and brown trout (+3·75 ± 1‰ for $\Delta\delta^{13}$C and +1·65 ± 1‰ for $\Delta\delta^{15}$N) were used following Cucherousset *et al.* (2007). The baseline for the prey stable isotope signal (mean ± SD) was calculated separately for each sampling site by pooling values of prey samples collected in April and June, 2015. The baseline was calculated to incorporate potential spatial variability in prey stable isotope values across the stream gradient and to match with consumer tissue turnover (Layman *et al.* 2012). We used the proportion of terrestrial prey in the diet as a representative diet score to test for an association of the diet with phenotypic traits. We assumed that a high proportion of terrestrial prey in the diet corresponds to a more pronounced drift foraging strategy, whilst a low proportion of terrestrial prey should correspond to a benthic foraging strategy, as terrestrial prey are proportionally more abundant in drift than at the bottom (Nakano & Furukawa-Tanaka 1994; Cucherousset *et al.* 2007). Comparison of proportion of terrestrial prey in the diet of brown and brook trout are reported in Appendix S3.

MORPHOMETRIC ANALYSES OF BODY SHAPE

Sixteen morphological landmarks were selected on the body of each individual, using photographs taken during the sampling in

April (see Appendix S2). Landmarks were digitized using tpsDig 2.10 and tpsUtil 1.38 programmes (Rohlf 2008). Body shape was adjusted for random individual body curvature during the photography, using the 'unbend specimen' function in tpsUtil (Rohlf 2008). The analysis of the body shape was performed in the R package 'GEOMORPH' (Adams & Otárola-Castillo 2013), using 14 landmarks (two of the landmarks were only used for the random curvature adjustment). Partial warps, which represent the non-uniform components of the shape variation, were constructed and further examined by principal component analysis (PCA). Consequently, each component of the PCA corresponded to one dimension of the shape represented by partial warps (Bookstein 1991). The first partial warp (PC1) explained 22·46% of variance, whereas subsequent partial warps explained a substantially lower proportion of variance (PC 2 12·87%, PC 3 11·40%, and PC 4 9·58%). Therefore, only PC1 was used in the subsequent analyses. High values of PC1 corresponded to high body height, relatively large head, and short tail (hereafter referred to as 'stout'), whilst low values of PC1 corresponded to a narrow elongated body with a relatively small head (hereafter referred to as 'fusiform') (see Appendix S2).

FISH HOUSING AND LABORATORY PROTOCOL

Brown trout were housed in holding tanks (30 L, 0·30 × 0·32 × 0·34 m, 10–11 individuals per tank) containing shelter (rocks, plastic tubes, and plastic plants) and aerated freshwater from a semi-recirculating flow-through filtration system (flow rate 2 L min^{-1}). Individuals from the sympatric and allopatric sampling sites were housed separately. Photoperiod followed natural light cycles and water temperature was kept at 11–13 °C throughout the laboratory experiments. Individuals were fed *ad libitum* during the whole period with a mix of chironomid larvae, maggots and earthworms. In order to allow evacuation of food contents and to standardize hunger levels, individuals were not fed during acclimation to behavioral scoring and respirometry (see details below). At the completion of the experiments, individuals were released back into the Ringsbäcken stream.

SCORING OF METABOLIC RATE – RESPIROMETRY

Fish were fasted for 4 days prior to respirometry. For this purpose, individuals were moved from the holding tanks to acclimation tanks, which had the same features as the holding tanks and contained groups of 8 individuals randomly selected from the holding tanks. Initially, fish were individually subjected to an exhaustive exercise protocol to elicit their maximum metabolic rate (MMR, Clark, Sandblom & Jutfelt 2013). Fish were chased for 3 min around a circular tank (diameter 0·3 m, water depth 0·2 m) containing 10 °C, aerated freshwater. All individuals were visibly exhausted by the end of the 3-min exercise period as highlighted by a lack of response to an experimenter tapping the caudal fin with the hand. Immediately following the exercise protocol (within 10 s), fish were individually placed into cylindrical, intermittent flow-through respirometers (volumes of 0·584 or 1·112 L depending on fish size) that were submerged in a reservoir bath, containing flow-through, aerated freshwater (10 °C). Upon fish entry, the respirometers were immediately sealed for 5 min and MMR was determined by measuring oxygen uptake, using best practices in intermittent flow-through respirometry (see Clark, Sandblom & Jutfelt 2013). Briefly, water was continuously circulated through each respirometer using an in-line submersible pump within a recirculation loop, and the oxygen concentration of the water in the respirometer was measured continuously at 0·5 Hz using a FireSting O_2 system (PyroScience, Aachen, Germany) calibrated in accordance with the supplier's manual. MMR was calculated from the decline in the partial pressure of oxygen in the water of the respirometers during the first 3 min of the 5-min sealed period following the exhaustive exercise protocol, as this represented the steepest linear decline in oxygen uptake for all individuals (i.e. slopes began to level off in some individuals after ~4 min and successive slopes became increasingly shallower as individuals recovered). Once MMR had been determined for each fish, the respirometers were equipped with automated flush pumps that refreshed the water in the respirometers for 5 min in every 20 min period, ensuring that oxygen levels in the respirometers always remained above 90% air saturation. Oxygen uptake was calculated during each 15-min period between flush cycles. SMR was calculated for each individual as the mean of the lowest 20% of oxygen uptake measurements taken during a period of ~18 h where the fish were left undisturbed after respirometer entry (Chabot, Steffensen & Farrell 2016). AS was calculated as the difference between MMR and SMR.

SCORING OF ACTIVITY – OPEN FIELD TEST

Fish were fasted in their holding tanks for 24 h prior to behavioral scoring in order to standardize individual hunger levels. The open field test trials were conducted in barren white rectangular plastic tanks (0·61 × 0·45 m, water level 0·10 m), positioned underneath a dim fluorescent light tube and a camera (Toshiba Camileo S20, Tokyo, Japan). When subjected to the trial, fish were gently netted from the holding tank and placed into trial tanks (one fish per tank). Individual activity was recorded for 10 min following 15 min of acclimation. Trial tanks were cleaned and refilled with fresh water for each trial. Trials were performed on 8 and 15 June 2015 from 08.00 until 17.00 under the same light (~100 lux) and temperature (~12 °C) conditions. Video recordings of fish movement were analyzed using automated tracking software, LoliTrack 4.0 (Loligo Systems ApS, Viborg, Denmark). Distance moved during the 10-min trial was measured as a proxy of activity for each individual (Adriaenssens & Johnsson 2013), this variable will hereafter be referred to as 'activity'. There were no strong indications of effects of time of day or scoring tank on the measured activity scores ($F_{7,84}$ = 1·2366; P = 0·2922; $F_{9,84}$ = 1·2192; P = 0·2944).

STATISTICAL ANALYSES

Although our investigations focused on a single cohort, individual phenotypic traits could be affected by body size. Therefore, residuals from a linear model between trait values and body length were used in all analyses to control for potential allometric effects (see Appendix S4). Multivariate correlation matrix of phenotypic and ecological niche traits pooled for all individuals (i.e. allopatric and sympatric sites together) was examined by PCA. The missing data in the correlation matrix were imputed using the regularised iterative PCA algorithm (Josse & Husson 2012). The significance of the difference between the groups and overall mean along the axes of principal components was tested by *v*-test, where absolute values of the test greater than 1·96 corresponds to a *P*-value less than 0·05 (Lê, Josse & Husson 2008). The shift in single phenotypic and ecological niche traits between allopatric and sympatric group was tested, using Welch *t*-tests. The adaptive integration among the phenotypic and ecological niche traits within the allopatric and sympatric groups was tested using a set of specific hypotheses on 13 selected pairs of traits (Table 1). The strength of the associations was tested using Spearman's rank correlation coefficient. To avoid type I errors associated with multiple comparisons, *P*-values of Spearman's rank correlations were adjusted for false discovery rate (Benjamini & Hochberg 1995). We compared the absolute effect sizes of correlations in allopatric and sympatric

Table 1. Description of presumably adaptive associations between 13 pairs of phenotypic and ecological niche traits used to test the strength of the adaptive phenotypic syndrome in allopatric and sympatric brown trout

Traits	Predictions	References
SGR ~ SMR	Individuals with a relatively high SMR grow faster in high food environments, but may lose their advantage when conditions deteriorate	Auer *et al.* (2015b), Metcalfe, Van Leeuwen & Killen (2016)
SGR ~ AS	Individuals with a high aerobic scope might reduce metabolic cost when conditions deteriorate and maximize metabolic performance when food is abundant; therefore AS may be positively correlated with growth	Auer *et al.* (2015a,b), Metcalfe, Van Leeuwen & Killen (2016)
SGR ~ Activity	Individuals with a high activity grow faster in high food environments, but may lose their advantage when conditions deteriorate	Adriaenssens & Johnsson (2011, 2013), Závorka *et al.* (2015)
SGR ~ body shape	Individuals with fusiform body shape have high swimming capacity, which allows them efficient food acquisition and territory defence; therefore they might grow faster	Boily & Magnan (2002), Ojanguren & Braña (2003)
Proportion of terrestrial prey in a spring and summer diet ~ activity	Active individuals are likely to be territorial and may adopt sit and wait strategy, which linked to feeding on terrestrial and aquatic prey from drift	Nakano & Furukawa-Tanaka (1994), Závorka *et al.* (2015)
Proportion of terrestrial prey in a spring and summer diet ~ body shape	Individuals with fusiform body shape are more likely to adopt active foraging strategy, which is linked to the feeding of benthic prey from bottom more than feeding on terrestrial and aquatic prey from drift	Nakano & Furukawa-Tanaka (1994), Ojanguren & Braña (2003)
Daily movement ~ activity	Individuals with high activity are likely to be territorial and keep position within a small but food rich patch of habitat (i.e. low daily moment), while passive individuals prefer non-territorial floater/wanderer strategy	Závorka *et al.* (2015)
SMR ~ activity	High activity can increase food income and deliver energy to digestive organs and muscles in high food environments, which increases SMR, but energetic demand of SMR may reduce activity when food is scarce	Careau & Garland (2012), Biro & Stamps (2010)
Daily movement ~ SMR	Individuals with high SMR are likely to be territorial and keep position within a small but food rich patch of habitat i.e. low daily moment), while passive individuals prefer non-territorial floater/wanderer strategy	Careau & Garland (2012), Slavík, Horký & Závorka (2014)
HR size ~ AS	Large oxidative window enables high physical performance to individuals with a high AS, and may facilitate movement within a large home range	Biro & Stamps (2010), Metcalfe, Van Leeuwen & Killen (2016)
HR size ~ body shape	High swimming capacity of individuals with fusiform body shape may facilitate movement within a large home range	Boily & Magnan (2002), Ojanguren & Braña (2003)

groups (i.e. Cohen's q), using paired t-tests to examine the hypothesis that integration of the phenotypic traits is stronger in the allopatric than in the sympatric group of brown trout. Statistical analyses were performed, using R 3.2.3 (R Core Team, Vienna, Austria).

Results

At the level of single phenotypic and ecological niche traits, there were significant differences between the allopatric and sympatric group in body shape ($|t| = 4{\cdot}4488$; $P > 0{\cdot}0001$; sympatric brown trout had stouter body shape), diet (spring season: $|t| = 3{\cdot}5115$; $P = 0{\cdot}0006$; summer season: $|t| = 2{\cdot}8620$; $P = 0{\cdot}0056$; sympatric brown trout consumed a higher proportion of terrestrial prey), and nearly significant differences in HR size ($|t| = 1{\cdot}8645$; $P = 0{\cdot}0648$; sympatric brown trout tended to have smaller home ranges). There were no significant differences in AS ($|t| = 0{\cdot}0294$; $P = 0{\cdot}9767$), SMR ($|t| = 0{\cdot}9082$; $P = 0{\cdot}3679$), activity ($|t| = 1{\cdot}5512$; $P = 0{\cdot}1251$), and daily movements ($|t| = 0{\cdot}3828$; $P = 0{\cdot}7030$).

We found a significant difference between the allopatric and sympatric group in the multidimensional space defined by key phenotypic and ecological niche traits (Fig. 2). The PCA yielded three dominant components summarizing 62·26% of the variation. PC1 (26·33%) corresponded predominantly to variation in the proportion of terrestrial prey in diet, PC2 (23·03%) summarized variation in SGR, body shape, and HR size, and PC3 (12·90%) corresponded to variation in AS (loadings of individual traits and eigenvalues of principal components are displayed in Appendix S5, Table S2). There was a significant difference between the allopatric and sympatric group along PC1 (v-test allopatric = $-3{\cdot}402$; sympatric = $3{\cdot}402$); however, we found a significant upstream gradient within the sympatric group along PC1, as the mean of the down-stream sympatric site was lower, and the means of the two upstream sympatric sites were greater than the overall mean (v-test sampling site 3 = $-3{\cdot}800$; sampling site 2 = $6{\cdot}834$; sampling site 1 = $2{\cdot}618$). There was a significant difference between the sympatric and allopatric group along PC2

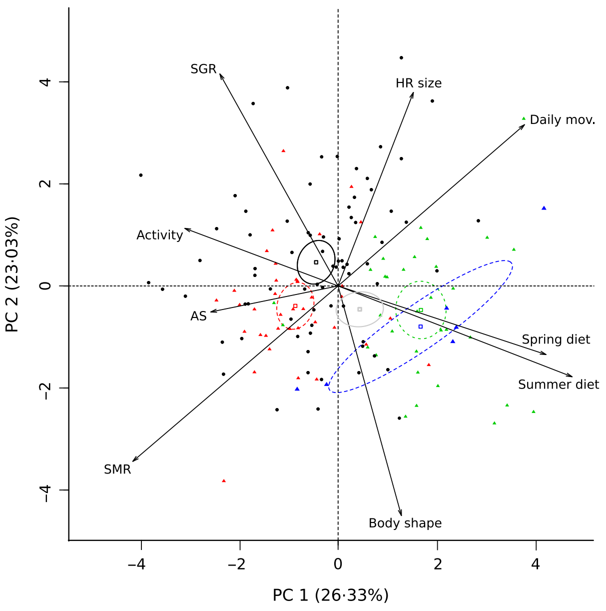


Fig. 2. Scatter plot showing the two largest components from the principal component analysis the multidimensional correlation matrix of phenotypic and ecological niche traits pooled for all individuals (i.e. allopatric and sympatric sites together). Sampling sites are represented by different colors (black – sampling site 4, red – sampling site 3, green –sampling site 2, and blue – sampling site 1). Circles denote individuals from allopatry and triangles denote individuals from sympatric sites. Empty squares correspond to mean of each group. Ellipses shows 95% CI of a group mean – black solid line ellipse represents allopatry, gray solid line ellipse represent sympatry (all 3 sympatric sampling sites pooled together), the dashed line ellipses correspond to the sympatric sampling sites 1, 2 and 3. Direction and relative importance of the measured traits is illustrated by the vectors. (Black – sampling site 4, dark gray – sampling site 3, medium gray – sampling site 2, and light gray – sampling site 1).

(*v*-test allopatric = 3·919, *v*-test = −3·919), but no substantial variation between the sympatric sampling sites along PC2 as their distance from the mean was similar (*v*-test sampling site 3 = −1·892; sampling site 2 = −2·120; sampling site 1 = −1·378). Neither was there any difference between the allopatric and sympatric group along the PC3 (*v*-test allopatric = −0·255, *v*-test sympatric = 0·255).

We found several significant correlations among the phenotypic and ecological niche traits in the allopatric brown trout (Fig. 3; Appendix S5, Table S3). Many of these were consistent with à priori predictions of how traits should be adaptively integrated (summarized in Table 1). In contrast, the integration of adaptive traits in sympatric trout was significantly weaker ($|t| = 2{\cdot}3285$; $P = 0{\cdot}0382$; Fig. 3). This breakdown of the adaptive phenotypic syndrome in sympatric brown trout was accompanied by a reduction in SGR in body length ($|t| = 2{\cdot}5996$; $P = 0{\cdot}01112$).

Discussion

Our results suggest that invasion from non-native brook trout results in a shift of a range of phenotypic and ecological niche traits in the sympatric native brown trout, when compared to allopatric brown trout. Moreover, the trait shifts in sympatric brown trout were linked to a breakdown of adaptive associations among phenotypic traits (Table 1), as suggested by a decrease in growth rate indicative of reduced fitness.

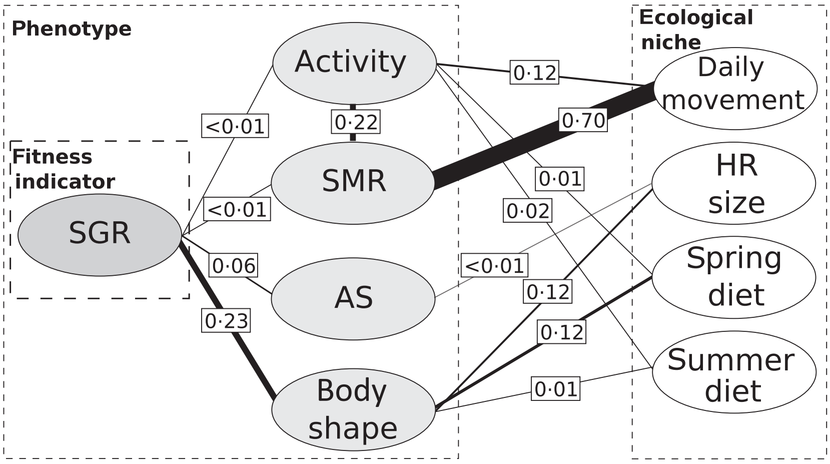
CONTRASTING PATTERNS OF TRAIT INTEGRATION IN SYMPATRIC AND ALLOPATRIC BROWN TROUT

We found an adaptive phenotypic syndrome integrating several key traits in the allopatric group of brown trout. Short daily movements of individuals, indicating stable position in the stream, were related to high SMR and activity. High activity and SMR are traits typically related to high-gain high-cost strategies, which are expected to be successful in a predictable environment with rich food resources (Biro & Stamps 2010). Therefore, it is likely that these three traits were associated with territorial behavior, where territorial individuals defend a small habitat patch, display high activity and SMR, whereas non-territorial floaters and wanderers display low activity and SMR (Jenkins 1969; Dingemanse & de Goede 2004; Careau & Garland 2012; Slavík, Horký & Závorka 2014). There was no relationship between SGR in body length and AS, but AS was positively correlated with SGR in body mass. This may support a positive association between the capacity for food consumption and AS, found by Auer *et al.* (2015a), but it also shows that individuals with high AS in the wild may not be able to better translate their energy reserves into growth of structural tissues than individuals with low AS (Auer *et al.* 2015b; Metcalfe, Van Leeuwen & Killen 2016). Moreover, we found that allopatric individuals with a fusiform body shape grew faster, had larger home ranges and consumed a lower proportion of terrestrial prey than individuals with a stout body shape. This could be explained by the higher sustained swimming capacity of trout with a fusiform body shape (Boily & Magnan 2002; Ojanguren & Braña 2003), which may facilitate exploration of new habitats and food acquisition. Actively moving individuals are also more likely to adopt an active foraging strategy linked to feeding on benthic prey from the stream bottom (Nakano & Furukawa-Tanaka 1994; Ojanguren & Braña 2003; Wilson & McLaughlin 2007). In contrast, integration of the phenotypic and ecological niche traits was negligible in brown trout living sympatrically with the invasive brook trout, which indicates the breakdown of the adaptive phenotypic syndrome in the sympatric situation.

POTENTIAL DRIVERS OF THE ADAPTIVE PHENOTYPIC SYNDROME BREAKDOWN

The allopatric group of brown trout only occurs downstream, whereas the abundance of brook trout increases in the upstream direction (see Appendix S1), which is a typical pattern of their sympatric distribution (Korsu, Huusko

(a) Allopatric group



(b) Sympatric group

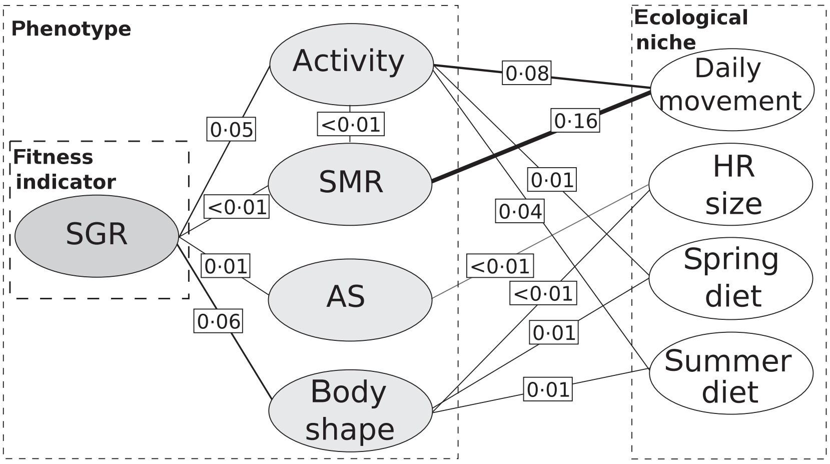


Fig. 3. Diagram shows strength of Spearman's rank correlation (ρ^2; shown in boxes) for 13 pairs of associations between measured traits in the allopatric group and sympatric group.

& Muotka 2007). This raises the question if the breakdown of the adaptive phenotypic syndrome and decrease in fitness of brown trout was only related to the presence of the non-native species or, at least partially, to other environmental factors associated with an upstream-downstream gradient (Killen *et al.* 2013). However, environmental drivers previously associated with the distribution and condition-dependent competition between the two salmonid species (i.e. water temperature, pH, presence of forest canopy, stream size, and bottom substrate; Korsu, Huusko & Muotka 2007; Korsu *et al.* 2012) were largely comparable across all our sampling sites, with the exception of the stream size, as the stream tends to be shallower and narrower in the upstream sections (see Appendix S6). Öhlund *et al.* (2008) have clearly shown (using data from 1000 sites across Sweden) that although brown trout can numerically dominate brook trout in sympatry even in the smallest streams, they are often unable to sustain viable populations once replaced by brook trout, which become numerically dominant due to their faster population growth rate. Fast population growth may be advantageous for populations living in an environment with occasional catastrophic events that cause either a decrease or extinction of local populations (Öhlund *et al.* 2008; Vincenzi *et al.* 2012), a phenomenon that may be more common in smaller headwaters. This mechanism may explain why brook trout are particularly successful in the upstream stretches of streams, as observed in this study and numerous others.

Non-native species often affect native species via competition for resources (e.g. food and shelter), and this is particularly true when the invader is closely related to the native species and their habitat requirements overlap (Cole & Harris 2011; Heavener, Carthey & Banks 2014). Certainly, inter-individual interactions between salmonid species are frequently driven by competition for resources and predation (McHugh *et al.* 2008; Näslund, Aldvén & Závorka 2015). However, non-native species can affect populations of native species even in the absence of direct competition or predation pressure, e.g. by influencing environmental complexity and stochasticity (Carpenter *et al.* 2011). Environmental changes induced by non-native species can impose novel selection pressures, which may indirectly eliminate individuals with certain phenotypic syndromes from a population (Cole & Harris 2011).

Fischer, Ghalambor & Hoke (2016) also demonstrate that the variability among phenotypes generally increases in populations exposed to novel environmental pressures. The latter alternative seems to fit with the findings of this and other studies (Korsu, Huusko & Muotka 2007; Öhlund *et al.* 2008), where dominant brown trout are negatively affected by closely related non-native brook trout, which are generally subordinate (Fausch & White 1981; Blanchet *et al.* 2007) and have a different ecological niche (Blanchet *et al.* 2007; Korsu *et al.* 2012).

We found that sympatric brown trout consumed a higher proportion of terrestrial prey upstream than downstream. Prey abundance was not quantified, thus we cannot rule out the option that prey availability affected this pattern. However, based on the findings of Syrjänen *et al.* (2011) comparing terrestrial prey input in small Scandinavian streams, we expected no substantial changes in terrestrial prey input along the stream gradient. Moreover, brook trout, which have previously been documented to have a higher preference for terrestrial prey than brown trout (Cucherousset *et al.* 2007) showed the opposite pattern in our study as they consumed less terrestrial prey overall and less upstream than downstream (see Appendix S3). In agreement with a previous study (Cucherousset *et al.* 2007), it is possible that the shift in brown trout diet toward terrestrial prey was linked to the increasing abundance of brook trout. We also found that sympatric brown trout had smaller home ranges, had a stouter body shape and grew slower than individuals in allopatry. The shift of these traits were not linked to the stream gradient, but clearly related to the presence of the non-native brook trout. Such a sharp shift in key phenotypic and ecological niche traits may be caused by plastic response of the traits to novel environmental pressures, which are induced by the behavior and ecological niche use of brook trout (Fausch & White 1981; Blanchet *et al.* 2007, 2008; Cucherousset *et al.* 2007). Dall, McNamara & Leimar (2015) have suggested that phenotypic variability in systems with an unstable environment and high gene flow (i.e. typical features of a salmonid population in a small stream) is driven mainly by maternal effect and the phenotypic plasticity of individuals responding to the pressures of the current environment. Interestingly, we only observed the breakdown of the correlations amongst traits in sympatric brown trout, and not the emergence of new ones. Therefore, it is possible that variation in the plasticity of phenotypic traits, can constrain the development of an optimal phenotypic syndrome (Pigliucci 2005; Ghalambor *et al.* 2007).

Conclusion

Defining the impact of non-native species at multiple levels of biological organization is a major challenge in ecology (Cucherousset & Olden 2011; Essl *et al.* 2015; Buoro, Cucherousset & Olden 2016). The novel findings from this study, which uniquely combines a wide range of measures from the field with standardized estimates in the laboratory, suggest that coexistence with a non-native species result in the breakdown of an adaptive phenotypic syndrome and an associated reduction in fitness of the exposed native population. The breakdown of the phenotypic syndrome was likely caused by differences in plasticity of individual traits (Dall, McNamara & Leimar 2015) in response to novel environmental pressures caused by the non-native species. The breakdown of adaptive phenotypic syndrome in native species is a potential mechanism underlying deleterious effects of non-native species in situations where no clear competitive pressure is apparent. Manipulative field studies are required to further address this interesting hypothesis.

Authors' contributions

All authors conceived the ideas and designed methodology and collected the data; L.Z. analyzed the data; L.Z. and J.I.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The data supporting this article have been archived at figshare.com (Data_Zavorka_et_al_2017_Func_Ecol; https://doi.org/10.6084/m9.figshare.3218740.v1) and published as part of the Supporting Information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Distribution of brook and brown trout in the study stream.

Appendix S2. Morphological landmarks and variance of body shape of brown trout.

Appendix S3. Dietary contribution of putative prey to brown and brook trout in each sampling site.

Appendix S4. Allometric models.

Appendix S5. PCA and full correlation matrix of phenotypic and ecological niche traits.

Appendix S6. Habitat characteristics.