









LETTER

Species divergence under competition and shared predation  

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Abstract

Species competing for resources also commonly share predators. While competition often drives divergence between species, the effects of shared predation are less understood. Theoretically, competing prey species could either diverge or evolve in the same direction under shared predation depending on the strength and symmetry of their interactions. We took an empirical approach to this question, comparing antipredator and trophic phenotypes between sympatric and allopatric populations of threespine stickleback and prickly sculpin fish that all live in the presence of a trout predator. We found divergence in antipredator traits between the species: in sympatry, antipredator adaptations were relatively increased in stickleback but decreased in sculpin. Shifts in feeding morphology, diet and habitat use were also divergent but driven primarily by stickleback evolution. Our results suggest that asymmetric ecological character displacement indirectly made stickleback more and sculpin less vulnerable to shared predation, driving divergence of antipredator traits between sympatric species.

KEYWORDS

adaptive divergence, asymmetric interactions, biotic selection, character displacement, sculpin, species interactions, stickleback

INTRODUCTION

While selection to lessen interspecific resource competition often drives divergence between species ('ecological character displacement'; e.g., Pfennig & Pfennig, 2009, 2010; Schluter, 2000a; Stuart et al., 2017), the consequences of other indirect species interactions are less understood (e.g., Brown & Wilson, 1956; Dayan & Simberloff, 2005; Grether et al., 2009; Schluter, 2000a, 2000b; Stuart & Losos, 2013; terHorst et al., 2018; Wootton, 1994). For example, species competing for similar food also often share predators (Cohen et al., 1990; Menge, 1995), and

theory suggests that predator-imposed natural selection on one prey species can be altered if that predator has access to another prey species (Abrams, 1998; Doebeli & Dieckmann, 2000; Holt, 1977; Holt & Lawton, 1994; Schreiber & Patel, 2015; Wootton, 1994). Indirect interactions via shared predators could thus be potent causes for adaptive change of species (Abrams, 2000; Brown & Vincent, 1992; Holt & Lawton, 1994).

Outcomes of shared predation may vary depending on the underlying mechanisms, including how shared predation interplays with competition (e.g., Abrams, 2000; Abrams & Chen, 2002a, 2002b; Abrams & Matsuda

1996; Holt & Lawton, 1994; Teixeira-Alves et al., 2016; van Baalen et al., 2001). For example, two co-occurring prey species might support higher predator densities, thereby increasing total predation and hence selection for increased defence in both prey species in sympatry. In contrast, antipredator traits of prey species might be selected in opposite directions if the vulnerability to predation relatively increases for one but decreases for the other species in sympatry (asymmetric risk). The general role of shared predation in diversification, and the relative prevalence of antipredator trait shifts in similar (unidirectional) versus opposite (divergent) directions between prey species remain open empirical questions (Abrams, 2000).

Here we investigate outcomes of shared predation in threespine stickleback (*Gasterosteus aculeatus*; hereafter ‘stickleback’) and prickly sculpin (*Cottus asper*; hereafter ‘sculpin’). These two fish species exist in a mosaic of allopatric and sympatric populations in small, postglacial lakes in British Columbia (Canada) and are preyed upon by an omnipresent and abundant predator, cutthroat trout (*Oncorhynchus clarkii*; hereafter ‘trout’) (Figure 1, Figure S1; Scott & Crossman, 1973). Previous research has shown that stickleback from lakes with and without sculpin are differentiated in several morphological and behavioural characteristics (Ingram et al., 2012; Miller et al., 2015; Rogers et al., 2012), and most genome-wide variation among stickleback from these lakes is explained by sculpin presence/absence (Miller et al., 2019).

Together, these findings suggest strong selective effects of sculpin on stickleback.

While sculpin and stickleback are likely to compete for shared resources when in sympatry (Bolnick et al., 2010; Ingram et al., 2012), sculpin may also prey occasionally on stickleback (Moodie, 1972; Pressley, 1981; see also Discussion). Yet, neither of the two previously conducted experiments found sculpin predation to directly affect antipredator traits of stickleback (Maccoll & Chapman, 2011; Miller et al., 2017). Instead, it is possible that sculpin influence antipredator traits of stickleback indirectly via trout. Whether stickleback have any selective effects on sculpin is unknown.

To investigate the effects of shared predation for two competing prey species, we compared shifts at ecologically relevant phenotypes between allopatric and sympatric populations of both stickleback and sculpin. First, we tested for unidirectional versus divergent shifts in antipredator traits between the species when sympatric. Then, we examined whether the species diverge in foraging traits, diet and habitat use in sympatry and how this niche divergence might influence their vulnerabilities to predators. We interpret observed antipredator trait shifts under possible alternative mechanisms, including the roles of indirect interactions via trout predation and resource competition. Overall, our study highlights shared predation as an indirect interaction that can drive divergence between competing species.

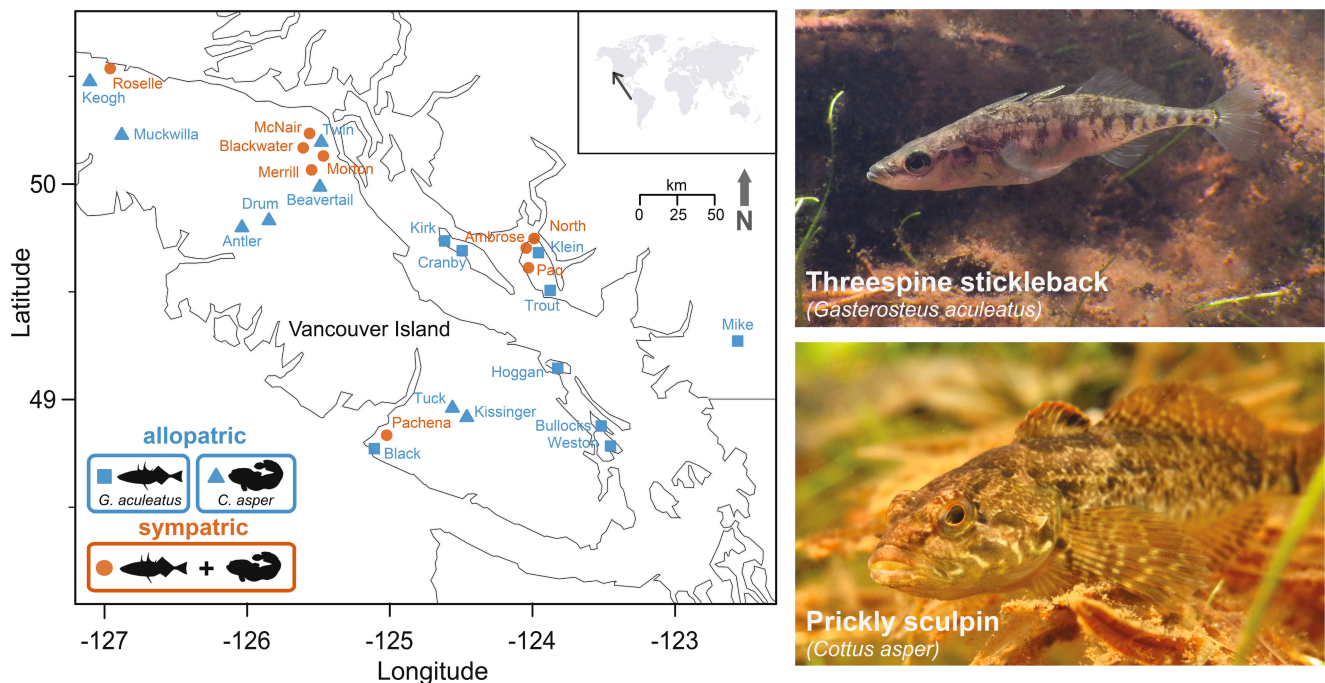


FIGURE 1 Study lakes and species. The map depicts the geographic location of the 26 study lakes and whether a lake is inhabited by stickleback but not sculpin (blue squares), by sculpin but not stickleback (blue triangles), or by both species (red circles). To the right, a threespine stickleback and a prickly sculpin in their natural habitat are shown (photos by M. Roesti). Cutthroat trout are common predators of both sculpin and stickleback (Figure S1) and present in all study lakes (Table S1).

MATERIALS AND METHODS

Study populations and fish sampling

We studied 18 stickleback and 17 sculpin populations from 26 small coastal lakes of southwestern British Columbia (Canada). Nine lakes had stickleback but no sculpin ('allopatric stickleback'), 8 lakes had sculpin but no stickleback ('allopatric sculpin'), and 9 lakes had both stickleback and sculpin ('sympatric' populations) (Figure 1, Table S1). Our study lakes were chosen such that (i) lakes of the three fish composition types were interspersed geographically to minimise other differences among them (our main study results proved robust when accounting for known abiotic variation among study lakes; see Discussion); (ii) populations from different study lakes have evolved independently since they established after the retreat of the Pleistocene ice sheets ~12,000 years ago (Bell & Foster, 1994; Dennenmoser et al., 2015; Miller et al., 2019); (iii) study lakes contain no other small fish species that could share trout as a predator together with sculpin and/or stickleback (see Supplementary Methods for further details).

All study lakes contain native cutthroat trout, which can prey on both stickleback and sculpin (Table S1, Figure S1, Scott & Crossman, 1973). Previous studies suggest that cutthroat trout is likely the single most important predator of stickleback (and other small prey fish) in small coastal lakes of British Columbia (Reimchen, 1990, 1992). Some lakes also have introduced rainbow trout (*Oncorhynchus mykiss*) (Table S1). Other large salmonid predators might be present currently or historically in some study lakes (Table S1), but they are unlikely to be abundant; we did not catch nor see these species during snorkelling, minnow trapping, and pole angling and neither did any of the local fishermen we talked to. Large avian piscivores such as loons are also present on study lakes, yet we have no reason to believe (but cannot rule out) that the three lake types would differ in this regard.

We sampled adult stickleback and sculpin between May and July 2015 and some in 2016 and took standardised pictures of the lateral body side of freshly killed sculpin specimens and of Alizarin Red-stained stickleback specimens (to better visualise bony armour traits) (see Supplementary Methods for details). Sample sizes were generally well balanced among populations and for the two sexes but varied slightly by analysis (see below and Tables S2 & S3).

Antipredator and foraging trait analyses

We tested for the effects of shared predation and competition by comparing putative 'antipredator traits' and 'foraging traits' between sympatric and allopatric populations of the two species.

For antipredator traits, we measured traits predicted to provide protection from trout predation. In stickleback, we measured: dorsal spine length, pelvic spine length, pelvic girdle length, and the number of lateral bony plates. These traits are known to protect stickleback against trout predation (e.g., Hagen & Gilbertson, 1972; Kitano et al., 2008; Lescak & von Hippel, 2011; Reimchen, 1980, 1990, 1992, 2000; Rennison et al., 2019). Antipredator strategies of sculpin are less known. We thus measured eight traits that we expected should be selected in sculpin to better defend against or escape attacks from large-gaped (trout) predators based on findings from other fish species (Bosher et al., 2006; Buser, 2020; Cowan, 1969; Hodge et al., 2018; Langerhans & DeWitt, 2004; Langerhans & Reznick, 2010; Price et al., 2015; Sfakiotakis et al., 1999; Wainwright & Longo, 2017; Webb, 1978): pre-opercular spine length, dorsal (fin) spine length, pelvic spine length, body width, peduncle depth, and the total area of the splayed second dorsal fin, anal fin and caudal fin (see Supplementary Methods for details).

For foraging traits, we measured the same four traits in both species: gill raker number, gill raker length, gape width, and premaxilla length (Supplementary Methods). These traits are known to influence feeding performance on different diets in stickleback (e.g., Berner et al., 2008, 2009, 2010; Kaeuffer et al., 2012; Lavin & McPhail, 1993; Robinson, 2000; Schluter & McPhail, 1992), as well as in other fish (e.g., Gerking, 1994; Motta, 1984; Wainwright & Richard, 1995). We note that substantial variation in the measured antipredator and foraging traits is known to be under independent genetic control in stickleback, thus allowing these traits to evolve independently from one another (e.g. Chhina et al., 2022; Peichel & Marques, 2017). While we do not know the degree to which trait variation is heritable in sculpin, trait correlations within sculpin populations were generally low, especially between antipredator and foraging traits, suggesting that these traits have the potential to independently respond to selection (Figure S2). Antipredator and foraging trait measurements were obtained for an average of 19 stickleback (total $N = 340$) and 21 sculpin (total $N = 356$) per population and trait (Tables S2 & S3).

Traits were positively associated with size (standard length). Thus, we followed Berner (2011) for size-correcting trait values prior to comparing populations (see Supplementary Methods for details). Briefly, we ran all samples per species and trait together in an ANCOVA with log-transformed 'trait' as response, 'population' as a factor, and log-transformed 'size' as a covariate. To obtain size-corrected individual trait values, we added residuals to the predicted trait value for each population at mean size across all individuals. We note that because the independent unit in our tests between lake types is the population and not the individual, our analyses are generally based on population means (Murtaugh, 2007).

We analysed general shifts in antipredator and foraging traits among study populations using Principal Component Analyses (PCA). PCA were run on size-corrected population means of all antipredator traits and all foraging traits per species on a log scale and rescaled to unit variance. Whenever there was a statistically well-supported difference ($p < 0.05$) in PC1 and/or PC2 scores between allopatric and sympatric populations within a species, we visualised these scores per population and averages thereof per lake type including non-parametric 95% confidence intervals. We evaluated the strength and direction (symmetry) of displacement in sympatry for every antipredator and foraging trait by comparing the larger grand mean trait value to the smaller grand mean trait value of the two population types in each species. To test the statistical significance of the difference between allopatric and sympatric population means for PC1, PC2, and each trait, we randomly reassigned the population labels within each species and compared the difference between sympatric and allopatric populations in 10,000 such permutations to the observed difference in the real data (Manly, 2007). Unless stated otherwise, we always calculated two-sided p -values through analogous non-parametric permutation procedures of population means (Murtaugh, 2007).

Body shape analysis

We know that fish body shape often evolves in response to predation and/or competition (Langerhans & Reznick, 2010), and for stickleback we also know that much variation in body shape is heritable (e.g., Peichel & Marques, 2017). We thus analysed body shape shifts with geometric morphometrics based on 21 (stickleback) and 19 (sculpin) fixed landmarks digitised on lateral body shape photographs from all populations (Figure S3 and Supplementary Methods). Following superimposition of landmark coordinates and removal of possible allometric effects, we assessed body shape shifts between allopatric and sympatric populations within each species using a Linear Discriminant Analysis (LDA) (see Supplementary Methods for details). The average sample size per population in this body shape analysis was 19 for stickleback (total $N = 335$) and 22 for sculpin (total $N = 374$).

Stomach content and stable isotope analyses

We analysed stomach contents of fish from all 35 study populations to test for ecological shifts between populations (see Supplementary Methods as well as Tables S4 & S5 for details). We used 'Proportional Similarity' (PS) (Bolnick et al., 2002; Schoener, 1968) to obtain

population-level shifts in diet overlap. We then tested whether interspecific diet overlap is increased or reduced in sympatry by comparing diet overlap in all pairwise comparisons of sympatric stickleback and sympatric sculpin populations ($N = 81$) to that of all pairwise comparisons of allopatric stickleback and allopatric sculpin populations ($N = 72$) (Supplementary Methods). We also ran an unconstrained Correspondence Analysis (CA) on the combined diet data set from the two species to examine multivariate diet divergence between allopatric and sympatric populations along the main axis of diet variation. To test for a (spatial) habitat shift between allopatric and sympatric populations, we classified prey items as either limnetic (i.e., prey found in the open water) or benthic (i.e., prey found in the littoral zone or sediments) (Berner et al., 2008; Bolnick et al., 2010; Harmon et al., 2009; Schluter & Mcphail, 1992). Following size correction of benthic diet proportions, we tested for a difference between lake types within each species using permutation. The average number of analyzed fish with non-empty stomachs per population was 16 for stickleback (total $N = 279$) and 15 for sculpin (total $N = 254$).

Stomach contents provide only a snapshot of an individual's diet. We thus also quantified the diet of 10 to 25 individuals from each of the 35 study populations using the ratio of nitrogen isotopes ^{15}N to ^{14}N ($\delta^{15}\text{N}$) from muscle tissue, which integrates the diet of an individual over recent months (Pinnegar & Polunin, 1999; Post, 2002) (see Supplementary Methods for details). Generally, higher $\delta^{15}\text{N}$ values indicate foraging on prey from a higher trophic level (Post, 2002), and in stickleback, higher $\delta^{15}\text{N}$ values indicate increased foraging on (predatory) open-water zooplankton relative to benthic macroinvertebrates (Arnegard et al., 2014; Kaeuffer et al., 2012; Matthews et al., 2010; Ostbye et al., 2016; Ravinet et al., 2013). We first standardised individual $\delta^{15}\text{N}$ values within each species for size and then used ANCOVA to test the effect of lake type on mean population $\delta^{15}\text{N}$ while controlling for baseline variation in $\delta^{15}\text{N}$ of lakes (this was only possible for 21 of our 26 total study lakes, see Results and Supplementary Methods). We also tested the prediction that the diet niche width of sympatric populations should be reduced compared to allopatric populations because of niche partitioning of the species in sympatric lakes. We used the among-individual stable isotope variance within a population as a proxy for a population's niche width (Bearhop et al., 2004), as calculated from size-corrected $\delta^{15}\text{N}$ values for all 35 study populations. The test accounted for a possible effect of variation in population means on within-population $\delta^{15}\text{N}$ variances (see Supplementary Methods for details). Finally, we tested the correlation between population means of $\delta^{15}\text{N}$ and each foraging trait and foraging PC1 and PC2 values using linear models. Baseline $\delta^{15}\text{N}$ of lakes was added as a covariate.

RESULTS

Divergent shifts of antipredator traits between the species in sympatry

Antipredator traits differed between allopatric and sympatric populations of both species, with shifts going in opposite directions between the species. In stickleback, the major PCA axis (PC1) for four antipredator traits explained 74.9% of the total trait variation and clearly separated allopatric and sympatric populations, with sympatric stickleback having increased antipredator trait values (permutation $p < 0.001$; Figure 2a, Figure S4). Antipredator PC2 did not separate allopatric from sympatric stickleback (permutation $p = 0.667$) but strongly separated the sympatric North Lake population from all other populations (Table S6). North Lake stickleback have a full set of armour plates along their body, which is exceptional for freshwater stickleback in our study area. When we considered each of the four antipredator traits individually, all of them were strongly and clearly differentiated between sympatric and allopatric stickleback populations (Figure 3; all permutation $p < 0.01$), with sympatric stickleback populations exhibiting, on average, a 118.9% increase in armour plating (without North Lake stickleback: 45.4%), a 38.4% increase in pelvic girdle length, a 62.0% increase in dorsal spine length, and

a 45.2% increase in pelvic spine length compared to allopatric populations.

Allopatric and sympatric populations of sculpin also showed shifts in antipredator traits. PC1 for the eight antipredator traits explained 48.4% of the total trait variation and separated allopatric from sympatric sculpin populations (permutation $p = 0.019$, Figure 2a). However, in contrast to stickleback, sculpin had decreased antipredator traits in sympatry (Figure 3, Figure S4). As in stickleback, the North Lake population was a biological outlier: antipredator morphology of the sculpin from this lake was among the most exaggerated of any sculpin population and by far the most exaggerated of all sympatric sculpin populations (Table S7), yet this lake does not appear special relative to other sympatric lakes in known abiotic or biotic characteristics (Table S1, see Discussion). Consequently, the statistical support for decreased antipredator traits in sympatric sculpin markedly increased when the North Lake population was excluded (i.e., the permutation p -value for antipredator PC1 was then 0.003).

When we considered each of the eight sculpin antipredator traits individually, we found all of them to be decreased in sympatric populations (Figure 3). For three traits, this decrease in sympatric populations was statistically well supported (permutation $p < 0.05$): anal fin area (8.4% decrease), dorsal spine length (5.0% decrease), and pre-opercular spine length (4.6% decrease).

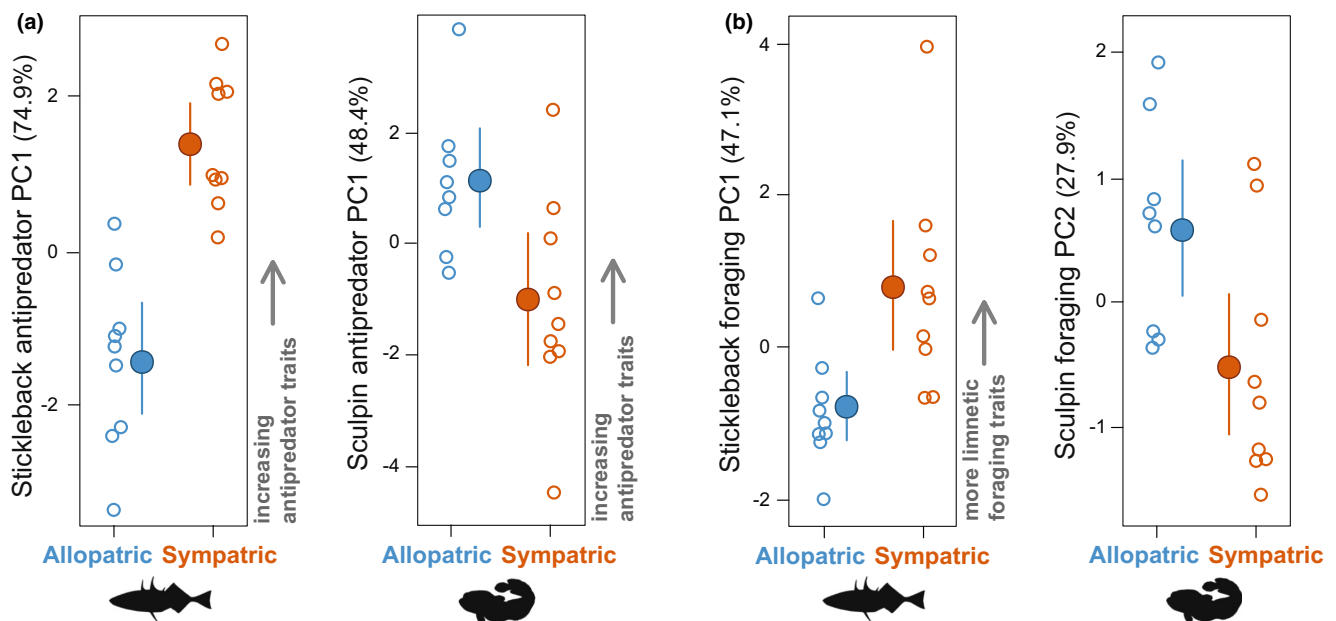


FIGURE 2 Overall shifts in antipredator and foraging morphology between allopatric and sympatric stickleback and sculpin. (a) Overall shifts in antipredator morphology in each species. Shown is the major axis of a principal component analysis (PC1) of all antipredator traits run separately for stickleback and sculpin. Open circles depict population means and filled circles indicate the grand mean per population type, surrounded by 95% CI. General shifts are indicated in grey on the right of each plot (see Figure S4 for details). Note that general shifts in antipredator morphology between allopatric and sympatric populations are in opposite directions between the species. (b) Overall shifts in foraging morphology in each species. For stickleback, PC1 from a principal component analysis of all foraging traits is shown, which clearly separates sympatric from allopatric populations. In sculpin, allopatric and sympatric populations only separate along foraging PC2, but not along PC1, which is why we show the former. All other plotting conventions in (b) are as in (a), except that general foraging trait shifts cannot as easily be summarised in sculpin.

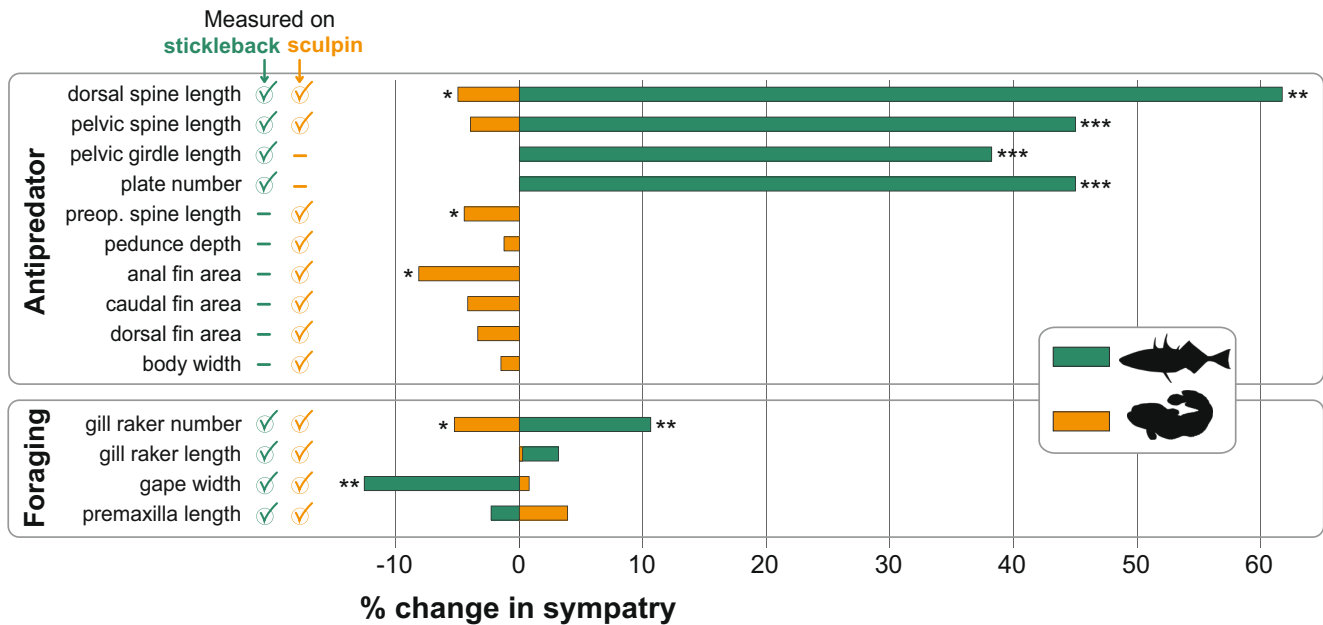


FIGURE 3 Direction and strength of trait-specific displacement in sympatry. Mean relative change of sympatric compared to allopatric populations of stickleback and sculpin at individual antipredator and foraging traits. Check marks next to trait names indicate that a specific trait was measured in a species. For ‘plate number’ in stickleback, the sympatric North Lake population was excluded from the calculation because it is the only known freshwater population in the study area with a full set of lateral armour plates. Including this population would inflate the mean increase in plate number of sympatric relative to allopatric stickleback populations from 45.4% to 118.9%. Statistical significance (the resampling p -value) is indicated for every trait as follows (see Table S8 for details): *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Table S8 also provides complementary significance statistics from analysing individual trait data instead of population means.

The decreases of individual antipredator traits of sympatric sculpin were again better supported (and also stronger) when excluding sculpin from the sympatric North Lake, with five of the 8 total traits reaching $p < 0.05$. For all traits, population (grand) means including 95% confidence intervals are provided in Table S6 (stickleback) and Table S7 (sculpin). We note that complementary model-based analyses of individual trait values confirmed the robustness of all trait shifts in both species (Table S8).

Asymmetric character displacement in foraging traits between the species

Character displacement in foraging traits occurred in both stickleback and sculpin, but shifts were much stronger in stickleback. PC1 for four foraging traits in stickleback explained 47.1% of the total trait variation and clearly separated allopatric and sympatric populations (permutation $p = 0.004$; Figure 2b, Figure S4). Of these four foraging traits, two showed statistically well-supported shifts: sympatric populations had, on average, 10.7% more gill rakers and 12.7% narrower gapes than allopatric populations (Figure 3).

Sympatric and allopatric sculpin populations separated along foraging trait PC2 (explaining 27.9% of the total variation; permutation $p = 0.029$; Figure 2b) instead of

PC1 (explaining 32.2% of the total variation; permutation $p = 0.736$), with foraging trait shifts generally occurring in opposite direction compared to stickleback (Figure 3). Of the four foraging traits, sympatric and allopatric sculpin populations only clearly differed in gill raker number ($p = 0.046$), with sympatric populations having 5.5% less gill rakers than allopatric populations (Figure 3).

Body shape shifts in both species

Shifts in overall body shape—which are not so easily separated into having only foraging or antipredator function—were apparent in both species but were again stronger in stickleback. The major axis of among-population body shape variation (LD1) in stickleback clearly separated allopatric from sympatric populations (permutation $p < 0.001$; Figure 4). Sympatric stickleback were more streamlined than allopatric stickleback, had larger eyes, a more upward-pointing mouth, and wider anal fins (Figure 4, Figure S5).

In sculpin, the major axis of among-population body shape variation (LD1) also separated allopatric and sympatric populations (permutation $p = 0.038$; Figure 4). Sympatric sculpin had shallower bodies, particularly at mid-body and caudal regions, the width of the second dorsal fin was reduced, and the mouth was more upward-pointing (Figure 4, Figure S5).

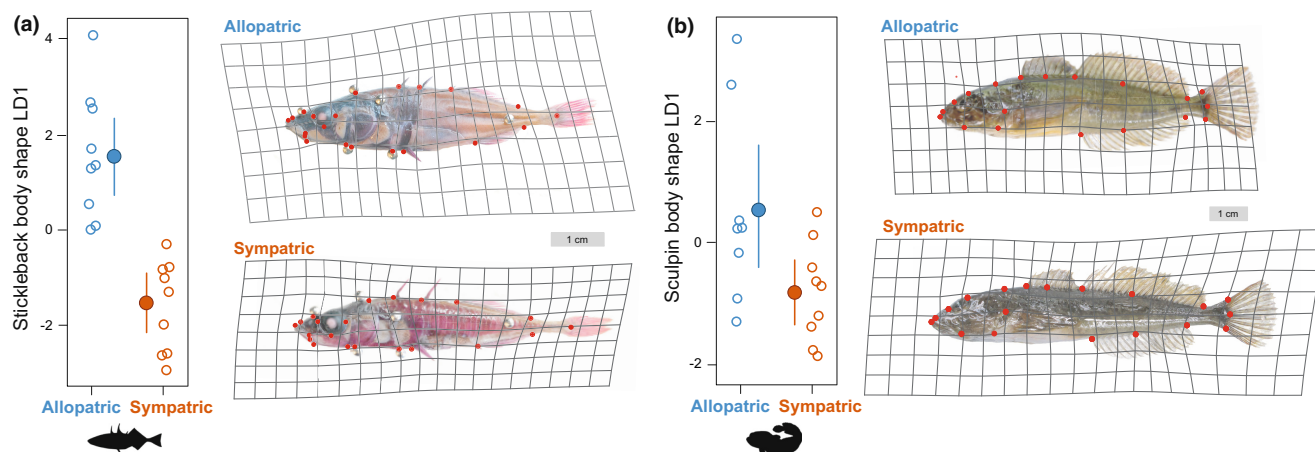


FIGURE 4 Body shape divergence between allopatric and sympatric populations of (a) stickleback and (b) sculpin. Mean landmark-based body shape per population (open circles) and the average per lake type (filled circles with 95% CI) along the major axis from a linear discriminant function analysis (LDA) run separately for stickleback and sculpin. The LDA was run grouping by population, but not by lake type. Two random specimens from the most extreme populations along LD1 are depicted, including red dots that indicate the position of the body shape landmarks. Deformation grids visualise shape shifts between the two depicted specimens in reference to each other. For average shape differences between allopatric and sympatric individuals of each species, see Figure S5.

Asymmetric shifts in diet and habitat use between the species

Average diet overlap between all pairwise comparisons of sympatric populations of sculpin and stickleback tended to be lower than between all pairwise comparisons of allopatric populations of sculpin and stickleback (permutation $p = 0.067$; Figure 5a, Tables S4 & S5). This pattern resulted from an asymmetric shift in diet between the species, thus matching the observed asymmetry in foraging trait divergence between the species. In stickleback, the mean proportion of benthic prey in sympatric populations was reduced by 29% compared to allopatric populations (permutation $p = 0.026$; Figure 5d), whereas there was little change (6%) in sculpin (permutation $p = 0.465$). Benthic prey dominated the sculpin diet everywhere (Figure 5d). Similarly, the major axis of variation from an unconstrained ordination of population diets (explaining 30.2% of the total diet variation) distinguished the two species (Figure 5b). Sympatric populations diverged, on average, when compared to allopatric populations, with stickleback exhibiting the larger shift (Figure 5b).

Diet shifts between allopatric and sympatric populations in both species were also evident in $\delta^{15}\text{N}$ signatures of muscle tissue, reflecting trophic position. Sympatric stickleback populations ($N = 8$) had higher $\delta^{15}\text{N}$ than allopatric stickleback populations ($N = 7$) ($F_{1,12} = 4.140$, $p = 0.065$; Figure 5c) reflecting increased foraging on open-water zooplankton (Arnegard et al., 2014; Kaeuffer et al., 2012; Matthews et al., 2010; Ostbye et al., 2016; Ravinet et al., 2013). Sculpin also shifted, but to a lesser degree, toward higher $\delta^{15}\text{N}$ in sympatric ($N = 8$) relative to allopatric ($N = 7$) populations ($F_{1,12} = 7.662$, $p = 0.017$; Figure 5c). While the variance in $\delta^{15}\text{N}$ among individuals within populations (‘niche width’) tended to be

lower in sympatric than allopatric populations of both species, this niche width reduction in sympatry received stronger statistical support in stickleback (stickleback: $F_{1,15} = 3.708$, $p = 0.073$; sculpin: $F_{1,14} = 2.462$, $p = 0.139$; see Figure S6).

Differences in resource use and foraging morphology were correlated among stickleback populations, but not among sculpin populations. In stickleback, $\delta^{15}\text{N}$ strongly predicted PC1 of all foraging traits ($F_{1,12} = 16.658$, $p = 0.002$; Figure S7) and populations with higher $\delta^{15}\text{N}$ values—indicating increased foraging of open-water zooplankton—had longer and more numerous gill rakers as well as narrower gapes (Figure S7). In contrast, neither PC1 nor PC2 of foraging morphology was associated with $\delta^{15}\text{N}$ among sculpin populations (PC1: $F_{1,12} = 1.187$, $p = 0.297$; PC2: $F_{1,12} = 0.025$, $p = 0.878$), although higher $\delta^{15}\text{N}$ was correlated with fewer gill rakers (Figure S7).

DISCUSSION

Indirect species interactions are thought to be potent sources of selection and thus important drivers of adaptive change. While many studies have focused on the effects of only interspecific resource competition, competition for shared food resources often goes hand in hand with sharing predators (Cohen et al., 1990; Menge, 1995). Yet, empirical investigations on how the addition of one competing prey species causes adaptive changes in antipredator traits in another competing prey species are lacking.

We evaluated the outcome of sympatry for competing species that share a predator by comparing allopatric and sympatric populations of both stickleback and sculpin in antipredator and foraging phenotypes. We were particularly interested in evaluating (i) whether shared

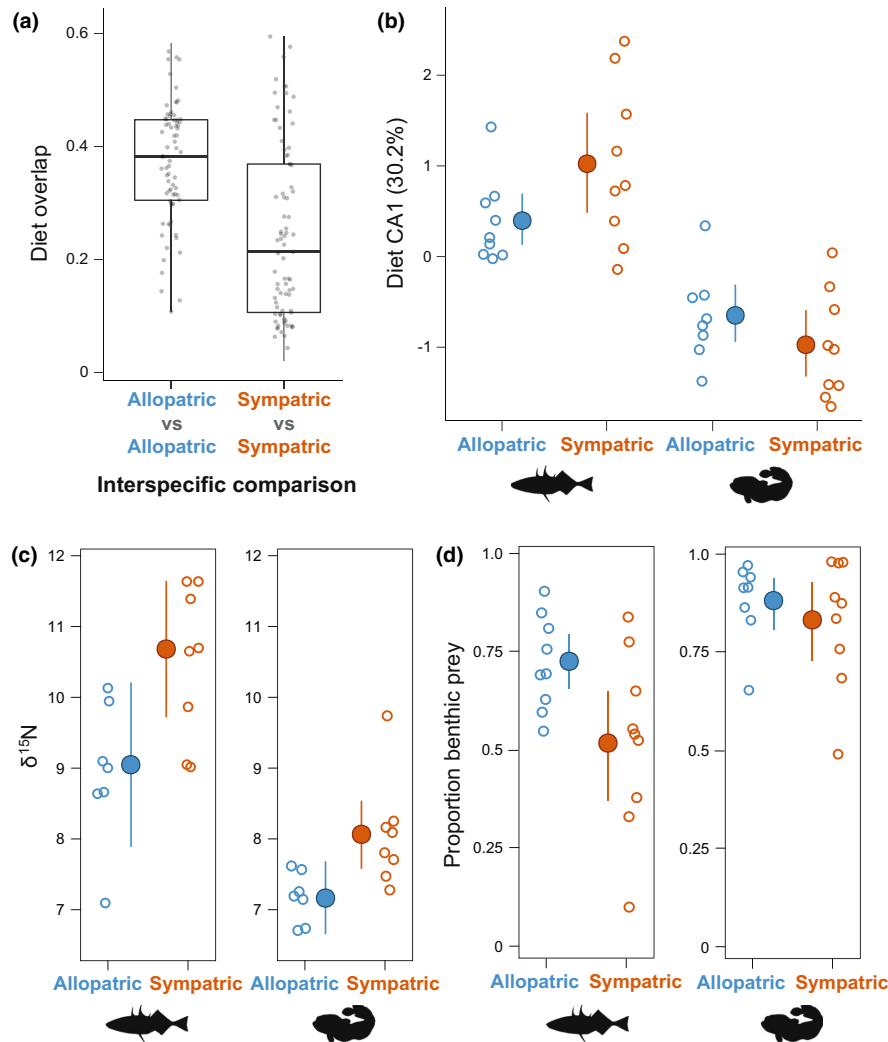


FIGURE 5 Diet and habitat shifts between allopatric and sympatric populations of stickleback and sculpin. (a) Diet overlap based on stomach contents for all pairwise population comparisons of allopatric stickleback vs. allopatric sculpin, and sympatric stickleback vs. sympatric sculpin. Boxplot boxes indicate the median and interquartile boundaries per comparison type. (b) The first axis of an unconstrained ordination of stomach contents including all stickleback and sculpin populations. Small open circles indicate average population diets, and large filled circles indicate mean diets across all populations per lake type and species. Higher CA1 scores mainly indicate increased foraging on Chydoridae and limnetic cladocerans, while lower CA1 scores are associated with increased foraging on benthic anisoptera nymphs and trichoptera larvae (see Tables S4 & S5 for more details) (c) $\delta^{15}\text{N}$ stable isotope signature of allopatric and sympatric populations of stickleback and sculpin after correcting for variation in baseline $\delta^{15}\text{N}$ among lakes. Open circles indicate partial residuals of population means and filled circles indicate means across all populations per lake type and species. (d) The average proportion of benthic prey consumed by allopatric and sympatric populations of stickleback and sculpin (open circles). Solid circles indicate the grand mean per lake type. Bars in panels b–d represent 95% CI.

predation favoured divergent or unidirectional shifts of prey defences in sympatry, and (ii) the presence of asymmetries in shifts caused by interspecific resource competition that might indirectly influence the outcomes of shared predation.

We found divergent shifts in antipredator traits between sympatric populations of the two species when compared with allopatric populations. Sympatric stickleback had increased defensive traits, whereas sympatric sculpin showed a decrease in pre-opercular and dorsal spines, as well as in fin and body traits putatively involved in behavioural escape from predators (Bosher et al., 2006; Cowan, 1969; Langerhans & DeWitt, 2004;

Langerhans & Reznick, 2010; Sfakiotakis et al., 1999; Webb, 1978). Much theoretical work proposes that antipredator traits of similar prey species should evolve in the same direction in sympatry relative to allopatry if sympatry relatively enhances (or diminishes) vulnerabilities in both prey species. Asymmetry between sympatric stickleback and sculpin in the vulnerability to predators might therefore explain why we observed divergent rather than unidirectional shifts in antipredator traits between the species (Abrams & Chen, 2002a, 2002b; Abrams & Matsuda, 1996; Holt & Lawton, 1994; Teixeira-Alves et al., 2016; van Baalen et al., 2001). How might such asymmetry arise?

We found morphological and diet evidence for asymmetric ecological character displacement between stickleback and sculpin, with more pronounced shifts in stickleback. Relative to allopatric stickleback, sympatric stickleback were shifted to foraging on limnetic prey and had typical morphological adaptations to foraging in the open water, including more gill rakers, narrower gapes, an upward-pointing mouth, and a more streamlined body (Berner et al., 2009, 2010; Hendry & Taylor, 2004; Reimchen et al., 1985; Robison, 2000; Schluter & McPhail, 1992; Walker, 1997; Webb, 1984; see also Ingram et al., 2012; Miller et al., 2017; Rogers et al., 2012). Accordingly, populations with a more limnetic foraging morphology had a more limnetic diet.

Additional evidence that these resource-related shifts in stickleback are driven, at least in part, by competition with sculpin for benthic food comes from the re-analysis of a previously conducted field experiment by Bolnick et al. (2010): stickleback placed for 15 days into enclosures in competition with small sculpin shifted to include more limnetic prey when compared to stickleback in sculpin-free enclosures ($p = 0.001$). This rapid shift resulted in reduced diet overlap of stickleback with sculpin ($p < 0.001$), much like what we found in natural populations (see Supplementary Analysis 1 for full details).

Compared to stickleback, sympatric sculpin shifted much less in foraging morphology and in the proportion of benthic prey in their diet compared to allopatric sculpin, and there was no strong association between foraging morphology and diet across sculpin populations. These relatively weak resource-related shifts in sculpin might be explained by sculpin being constrained to feeding on bottom-dwelling prey due to their lack of a swim bladder (Buser et al., 2019; Goto et al., 2014; Norton, 1991; Tolmacheva, 2010; but see Ricker, 1960, Woodruff & Taylor, 2013).

An intriguing possibility, therefore, is that the asymmetric habitat shifts driven by resource competition contributed to divergence of antipredator traits between the species in sympatry, by causing the vulnerability to predation to increase for one species but decrease for the other species. That is, the shift of sympatric stickleback to the open-water niche likely increased their exposure to trout predation, selecting stickleback to be more heavily armoured as a post-capture defence mechanism (Hagen & Gilbertson, 1972; Lescak & von Hippel, 2011; Reimchen, 1980, 2000; Rennison et al., 2019). Indeed, this idea can explain why stickleback have (i) retained more armour from their more heavily armoured marine ancestors in lakes with sculpin, and (ii) evolved to exploit the relatively safer benthic habitat in the absence of sculpin (Rudman et al., 2016; Vamosi & Schluter, 2002). However, increased vulnerability of stickleback to trout in sympatric lakes does not by itself explain the reduced antipredator traits of sympatric sculpin, which did not undergo a habitat shift. Instead, we propose that the increased use of open water by stickleback has led trout to specialise on

them, leading to reduced predation on benthic sculpin and hence relaxed selection for antipredator traits (Teixeira-Alves et al., 2016; van Baalen et al., 2001). Indeed, available data from trout stomach contents from previous and our own fishing efforts clearly support this idea: while there was no evidence for trout predation on sculpin in any of the 5 sympatric lakes with available trout stomach information, trout were found to have preyed on sculpin in all of the 6 surveyed lakes without stickleback (Table S9).

Intraguild predation—when competitors eat each other—may cause an additional asymmetry between the two species in sympatry. While stickleback do not prey on other fish (except occasionally eating fish eggs) and thus cannot directly cause antipredator trait shifts in sculpin, direct sculpin predation on stickleback and their eggs is known and could explain the slightly elevated $\delta^{15}\text{N}$ of sympatric compared to allopatric sculpin (Maccoll & Chapman, 2011; Moodie, 1972; Pressley, 1981). However, predation by sculpin is unlikely to be the main driver of the habitat shift and the increased antipredator traits we observed in sympatric stickleback because (i) sculpin too small to prey on stickleback were experimentally found to drive the habitat shift of stickleback observed in nature (Supplementary Analysis 1), (ii) sculpin predation on stickleback adults was rare based on stomach contents from sympatric sculpin, (iii) sympatric sculpin do not seem morphologically adapted to be efficient predators of stickleback, and (iv) neither of two previous experimental tests found sculpin predation to select for increased defensive traits in stickleback (Maccoll & Chapman, 2011; Miller et al., 2017) (see Supplementary Discussion for a more detailed examination of these and further points). Elevated $\delta^{15}\text{N}$ of sympatric sculpin is thus best explained by sculpin occasionally preying on stickleback eggs or fry, but not stickleback adults. Thus, while we cannot rule out any contribution of direct sculpin predation to antipredator trait shifts or of a perceived threat of sculpin to foraging shifts of sympatric stickleback, sculpin predation is neither a likely nor a sufficient explanation for those shifts.

Synthesis and general implications

In light of theory and our results, we propose that divergence of antipredator traits between the sympatric prey species studied here is a consequence of their asymmetric interactions including shared predation. We propose a history in which asymmetric ecological character displacement in sympatry led indirectly to increased trout predation on stickleback but decreased trout predation on sculpin, compared to lakes where each species occurs in the absence of the other. Thus, despite little obvious effects of competition for sculpin, the strong effects of competition for stickleback might have led indirectly to divergent selection on, and thus the adaptive change of, antipredator traits between sympatric and allopatric sculpin.

While the results from our comparative study proved robust to possible confounding abiotic and biotic variation among study lakes (Supplementary Analysis 2), we acknowledge that the proposed mechanism to explain divergence in antipredator traits between competing prey species in sympatry requires further experimental study. Nevertheless, additional evidence comes from shifts previously observed in defensive traits between sympatric species of threespine stickleback. In a handful of so-called ‘stickleback species-pair lakes’ in British Columbia (Canada)—which all have (or had) trout but no sculpin—the limnetic stickleback ecotype occupying the open water is more heavily armoured, whereas the Benthic ecotype from the littoral zone has extremely reduced armour compared to populations occurring as single stickleback species in otherwise similar lakes (Schluter & Mcphail, 1992; Vamosi & Schluter, 2004). As in the sympatric stickleback-sculpin lakes, the more benthic species in the stickleback species-pair lakes may have evolved reduced armour because the presence of the limnetic species in the open water led trout to become more specialised on them, thereby reducing predation on the benthic species (Vamosi & Schluter, 2002).

Overall, our findings emphasise the importance of indirect species interactions beyond resource competition in driving divergence of species. Our results also caution that in nature, the effects of various species interactions cannot be understood independently from one another (terHorst et al., 2018). In the system examined here, the effect of trout predation on sculpin sympatric with stickleback appears to depend both on the effects of competition between the prey species as well as on the asymmetry of the consequent shared predation. This scenario is contrary to the prevalent idea that shared predation is reciprocally negative (−/−) between prey species, but instead suggests that asymmetric interactions can result in mixed (+/−) effects of predation on prey species in sympatry. Given that competitors commonly share predators and that the effects of competition are often asymmetric for species (Schluter, 2000a), shared predation could be a common additional driver of divergence of species.

AUTHOR CONTRIBUTIONS

MR conceived and oversaw the study, conducted the fieldwork, designed and carried out the analyses, interpreted and visualised the results, and wrote the original manuscript. JSG helped with designing and conducting analyses. JSG, SB, PR, MH and MR phenotyped fish. DIB and YES provided a preliminary re-analysis of Bolnick et al. (2010). DS helped with designing analyses and, together with YES, contextualising this study. DS provided, together with CLP, funding to conduct research. All authors contributed to interpreting results and revising the manuscript.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

PEER REVIEW

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OPEN RESEARCH BADGES



This article has earned Open Data and Open Materials badges. Data and materials are available at: <https://doi.org/10.5061/dryad.wwpzgmsnn>.

DATA AVAILABILITY STATEMENT

Raw data supporting the main results and code is archived in Dryad under <https://doi.org/10.5061/dryad.wwpzgmsnn>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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