

# Stable isotope niche convergence in coexisting native and non-native salmonids across age classes

Julien Cucherousset, Libor Závorka, Sergine Ponsard, Régis Céréghino, and Frédéric Santoul

**Abstract:** Niche divergence resulting from coevolution is commonly believed to favour coexistence among competing species; however, recent investigations have demonstrated that an unexpected niche convergence can occur when native and non-native species coexist. Yet, our understanding of the ontogenetic characteristics of this niche convergence remains limited. In the present study, we quantified the stable isotope niche of native brown trout (*Salmo trutta*) in allopatry and sympatry with non-native brook trout (*Salvelinus fontinalis*) across four age classes. Our results demonstrated that brown trout displayed a stable isotope niche closer to brook trout in sympatry than in allopatry, which was likely driven by an increased consumption of terrestrial invertebrates by sympatric brown trout. Stable isotope niche overlap was the strongest for young-of-the-year individuals and the intensity of overlap between sympatric native brown trout and non-native brook trout decreased during ontogeny. These findings indicate that niche convergence between the species occur at the earliest age class of the native species and are maintained across ontogeny.

**Résumé :** La divergence de niche est une mécanisme qui favorise la coexistence des espèces mais des travaux récents ont démontré qu'une convergence de niche pouvait se produire lorsque des espèces natives et non-natives coexistaient. A ce jour, notre connaissance de la mise en place de cette convergence au cours de l'ontogénie reste néanmoins limitée. Dans cette étude, nous avons quantifié la niche isotopique de quatre classes d'âge d'une espèce native, la truite commune (*Salmo trutta*), vivant en allopatrie et en sympatrie avec une espèce non-native, l'omble de fontaine (*Salvelinus fontinalis*). Nos résultats démontrent que la truite commune présente une niche isotopique plus semblable à celle des ombles de fontaine en sympatrie par rapport à sa niche isotopique en allopatrie et que cela est probablement causé par une plus forte consommation d'invertébrés terrestres par les truites communes en sympatrie. Le chevauchement des niches isotopiques est le plus important pour les juvéniles de l'année, et l'intensité du chevauchement entre truites communes et ombles de fontaine en sympatrie diminue au cours de l'ontogénèse. Ces résultats indiquent que la convergence de niches se produit dès la toute première classe d'âge de l'espèce native et se poursuit durant toute la vie des individus.

## Introduction

Biological invasions can provide new insights into our understanding of species coexistence because co-evolutionary history is lacking in novel communities resulting from human introductions of non-native species (Cadotte et al. 2006). Stable coexistence of native and non-native species can occur when non-native species colonize a “vacant niche” or when rapid niche shifts limit the overlap in resource use by native and non-native species (Hardin 1960). Phylogenetically closely related species often have similar niches, and thus introduction of a such non-native species can expose native species to strong novel competition pressure (Blanchet et al. 2008). Competition for shared resources could be associated with a reduced fitness of less competitive species (Leger and Espeland 2010). Quantifying the intensity of niche differences between related native and non-native species in the wild is therefore needed to improve our knowledge on the mechanisms allowing species to coexist.

An interesting example to investigate this question is the coexistence of native brown trout (*Salmo trutta*) with non-native brook trout (*Salvelinus fontinalis*) in Europe. The European brown trout and the North American brook trout are two salmonid species that have been reciprocally introduced into Europe and North America (Rahel 2007; Korsu et al. 2007). When introduced into

North America, *S. trutta* displaced native *S. fontinalis* towards upstream headwaters (Fausch and White 1981; Wagner et al. 2013), whereas introduced *S. fontinalis* excluded native *S. trutta* from upstream sections and small tributaries in Europe (Korsu et al. 2012). These partial displacements of the native species by the non-native species indicate the existence of interspecific competition for similar and limiting resources. While native brown trout has generally higher preference for aquatic than terrestrial prey compared with non-native brook trout (Syrjänen et al. 2011), recent investigations in Europe have evidenced unexpected trophic interactions between the two species. Horká et al. (2017) found that the proportion of terrestrial and aquatic prey in stomach contents of adult native brown trout coexisting with non-native brook trout did not differ from allopatric situation in Czechia. In contrast, using stable isotope analyses (SIA), Cucherousset et al. (2007) found that the stable isotope niche of the two species converged when coexisting in French streams, with adult native brown trout shifting their diet towards a higher consumption of terrestrial prey when coexisting with brook trout. A similar convergence was also observed for age-1 brown trout sympatric in Swedish streams (Závorka et al. 2017). This larger diet overlap between the two coexisting species, indicates the unexpected niche convergence,

Received 24 May 2019. Accepted 14 April 2020.

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**Table 1.** Fish density estimates (with upper and lower values in parentheses) and habitat characteristics (mean with SE in parentheses) in the two stream stretches.

Variable		Allopatric section	Sympatric section
No. of fish captured	<i>S. trutta</i>	98	81
	<i>S. fontinalis</i>	0	53
Density estimates (individuals·10 m <sup>-2</sup> )	<i>S. trutta</i>	2.31 (2.14–2.48)	0.93 (0.88–0.97)
	<i>S. fontinalis</i>	0.00 (0.00–0.00)	0.74 (0.69–0.79)
No. of measurements		23	41
Substratum <sup>a</sup>	Silt (%) <sup>NS</sup>	0.0 (0.0)	2.1 (0.8)
	Sand (%) <sup>NS</sup>	0.4 (0.4)	0.0 (0.1)
	Gravel (%) <sup>NS</sup>	23.0 (6.1)	15.2 (3.9)
	Pebble (%)**	54.8 (6.8)	32.9 (5.4)
	Cobble (%)*	21.7 (6.1)	49.5 (6.6)
	Substratum score <sup>b,*</sup>	3.0 (0.1)	3.3 (0.1)
Channel	Length (m)	90	198
	Depth (cm) <sup>NS</sup>	18.3 (1.4)	22.0 (1.7)
	Width (m) <sup>NS</sup>	5.1 (0.2)	5.1 (0.3)
	Velocity (m·s <sup>-1</sup> ) <sup>NS</sup>	0.51 (0.08)	0.33 (0.05)

**Note:** Statistical significance is provided as superscript for between sections comparisons (Mann–Whitney test: NS, non-significant; \*, <0.05; \*\*, <0.01).

<sup>a</sup>Determined visually according to a modified Wentworth grain-size classification: silt (<0.06 mm), sand (0.06–2 mm), gravel (2–25 mm), pebble (25–50 mm), and cobble (>50 mm).

<sup>b</sup>Calculated using the following score for each grain size (0: silt, 1: sand, 2: gravel, 3: cobble, and 4: pebble).

which was not a site-specific process and requires deeper investigations.

The existence of diet convergence between native and non-native species has been reported in several taxa. For instance, Cole and Harris (2011) observed diet convergence in native adult day gecko (*Phelsuma ornata*) in Mauritius, which adjusted their diet towards larger overlap with non-native house gecko (*Hemidactylus frenatus*) in the seasons when prey abundance was the highest. These findings are, overall, in conflict with competitive exclusion principle, as higher trophic overlap between native and non-native species should increase the intensity of interspecific competition (Hardin 1960). Yet, our understanding of the mechanisms leading to this trophic convergence remains limited, primarily because studies evaluating niche convergence between native and non-native species have mostly focused on adults. Since ontogenetic diet shifts occur in many species (Shine and Sun 2003; Nunn et al. 2012), determining when trophic convergence occurs during ontogeny is an important knowledge gap that should be filled.

In the present study, we aimed to quantify the stable isotope niche (size and overlap) of native brown trout and non-native brook trout across age classes. We also tested whether coexistence with non-native brook trout affects the body condition of native brown trout in different age classes.

## Methods

### Study area

The study was conducted in an upstream stretch of the Oriège River (southwestern France, 1°57'E, 42°39'N) that hosts a population of native brown trout (*S. trutta*). Brook trout (*S. fontinalis*) were introduced there in the 1950s, and no other fish species than these two salmonids occur in this stretch. Brook trout have established self-sustained populations (no stocking for at least 20 years; Cucherousset et al. 2007), and the two species have also been reported to interact reproductively and hybridize, as observed in the study site during sampling, but frequency of hybrids in the population is extremely low (Cucherousset et al. 2008). The stream stretch was divided into two noncontiguous sections: the “allopatric” section located downstream with brown trout only and the “sympatric” section located upstream containing both species (details available in Cucherousset et al. 2007). The sections were surrounded by a similar landscape and had, overall, similar channel characteristics (width, depth, and water velocity), except that the

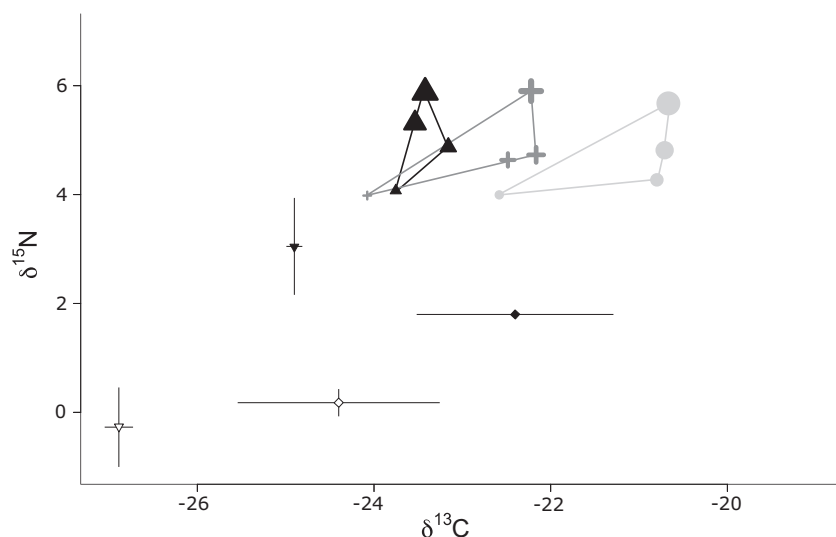
sympatric section had a substrate with a higher proportion of cobble (Table 1). Total fish density was slightly higher in the allopatric section compared with the sympatric sections (Table 1), indicating that the presence of brook trout decrease brown trout density, as observed elsewhere (Öhlund et al. 2008).

### Sampling and stable isotope analyses

In June and September 2007, the two sections were sampled by electrofishing using a backpack electroshocker (EFGO FEG 1500, Germany) and a two-pass removal approach. Sampled fish were anaesthetized with 2-phenoxy-ethanol (0.04 mL·L<sup>-1</sup>) before being measured (total length, TL), weighed, and clips of the tip of the left pelvic fin (Hayden et al. 2015) were taken. TL did not differ significantly between sections nor between species ( $F_{[2,147]} = 0.2631$ ;  $p = 0.769$ ) for the 50 fin-clipped individuals for each species and section ( $n_{\text{total}} = 150$ ) that were subsequently analysed for SIA in June. Although turnover can vary between species (e.g., Busst and Britton 2018), SIA of fin clips collected in June provide information about the trophic niche of fish in spring. In June, young-of-the-year (YoY) age-0 individuals were recently hatched and might have shown maternal stable isotope values (Doucet et al. 1999). Consequently, YoY individuals were sampled later in September, and SIA of fin clips of these individuals provide information about the trophic niche of fish in summer. In each section, 13 YoY brown trout with similar TL were sampled along with four age-0 brook trout. Clips of pelvic fin were used for SIA because their stable isotope values and turnover correlate closely with those of muscle tissue in salmonids and allow nonlethal sampling (Jardine et al. 2005b). Fish samples for SIA were oven-dried at 60 °C for 48 h and ground to a homogeneous powder using a mixer mill. SIA were conducted at the Stable Isotopes in Nature Laboratory, University of New Brunswick, Canada. Lipid content can affect the stable isotope values of consumers, and C:N ratio is a good indicator of lipid content (Post et al. 2007). The C:N ratio of fish samples was overall low and homogeneous (mean =  $3.62 \pm 0.16$  SD), indicating a low lipid content (Post et al. 2007) and did not differ significantly between allopatry and sympatry stretches for brown trout ( $3.56 \pm 0.12$  and  $3.57 \pm 0.14$ , respectively;  $W = 1054.5$ ,  $p = 0.179$ ).

Fish were divided into four age classes based on TL according to the expected growth rate and age–length relationship observed in previous studies of salmonids in oligotrophic streams (Öhlund et al. 2008; Závorka et al. 2013). Based on the size distribution

**Fig. 1.** Stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) convex hull areas of allopatric brown trout (light grey line), sympatric brown trout (dark grey line), and sympatric brook trout (black line). Convex hull polygons are based on centroids of  $\text{SEA}_b$  ellipses for specific age classes (the smallest symbols for young-of-the-year and the largest symbols for adult-age-3+) and sections and species (symbol types: allopatric brown trout = filled circles, sympatric brown trout = bold crosses, sympatric brook trout = filled triangles). Mean ( $\pm\text{SE}$ ) stable isotope values of potential prey are illustrated for terrestrial herbivores ( $n = 5$ , white inverted triangle), terrestrial predators ( $n = 4$ , black inverted triangle), aquatic herbivores ( $n = 8$ , white diamond), and aquatic predators ( $n = 5$ , black diamond).



observed in the present study, the length ranges for each age class were as follows: YoY-age-0: TL = 39–84 mm sampled in September; parr-age-1: TL = 57–109 mm in June; parr-age-2: TL = 110–174 mm in June; adults > age-3: TL = 175–255 mm in June. Note that while length ranges of YoY-age-0 in September and parr-age-1 in June overlap; in September when YoY-age-0 were sampled, parr-age-1 were distinctively larger than YoY. These age classes were also confirmed by the reading of the scales of some individuals from the studied area. Body condition of individuals was inferred from length–weight relationship calculated as residual mass from a linear model between individual body mass (log-transformed) and TL (log-transformed) (Acou et al. 2008).

Previous investigations have revealed that invertebrates (benthic abundance and drift) were overall highly abundant across the stretches (benthos: 16 713 ( $\pm 6351$  SE) individuals·m<sup>-2</sup>; drift: 10.96 ( $\pm 8.41$ ) and 1.93 ( $\pm 0.46$ ) aquatic and terrestrial individuals·m<sup>-3</sup>, respectively) and that there was no spatial patterns in their abundance along the upstream–downstream (Aymes 2005). The aquatic and terrestrial invertebrate taxa consumed by fish were known from previous studies conducted in this river (Lagarigue et al. 2002; Aymes 2005; Cucherousset et al. 2007). Potential prey specimens were collected in June 2007 at randomly selected locations in the two sections using hand nets. Invertebrates were identified as belonging to 10 taxonomic groups. These taxa were then partitioned into four functional feeding groups adapted from Merritt and Cummins (1996): (i) aquatic herbivores (one grazer (*Ecdyonurus* spp., Ephemeroptera), one filter feeder (Simuliidae, Diptera), one shredder (*Leuctra* spp., Plecoptera), and one scraper (*Rhithrogena* spp., Ephemeroptera)) and (ii) aquatic predators (Limoniidae, Diptera and *Perla* spp., Plecoptera). We also considered two groups of terrestrial invertebrates known to commonly fall into temperate streams and to be consumed by salmonids (e.g., Baxter et al. 2005): (iii) terrestrial herbivores (Coleoptera, Orthoptera) and (iv) terrestrial predators (Araneida, Formicidae). Terrestrial invertebrates were kept alive for 24 h to ensure gut clearance and then killed by freezing, while the guts of aquatic predators were removed before processing (as per Jardine et al. 2005a). Specimens were then subjected to SIA as pooled samples (mean  $\pm$  SE = 9.25  $\pm$  1.99 individuals) for each taxonomic group. All samples were oven-dried at 60 °C for 48 h and ground to a homogeneous powder using a

mixer mill. In total, 22 samples of invertebrates were analysed: eight samples of aquatic herbivores, five samples of aquatic predators, five samples of terrestrial herbivores, and four samples of terrestrial predators. Differences between the two sections were tested using paired *t* tests, both at the taxonomic and at functional group levels. No differences in stable isotope baseline values between the two sections (caused by, e.g., tributary confluences, forest inputs, or human disturbances) was found. Specifically, there was no significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for invertebrate taxonomic groups (paired *t* test,  $df = 9$ ,  $t = 1.402$ ,  $p = 0.194$  and  $t = 1.260$ ,  $p = 0.239$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) and functional groups (paired *t* test,  $df = 6$ ,  $t = 1.485$ ,  $p = 0.234$  and  $t = 0.772$ ,  $p = 0.496$ , respectively) between the two stream stretches.  $\delta^{13}\text{C}$  was more variable for aquatic invertebrates than for terrestrial invertebrates (Fig. 1); however, this variation was unlikely to affect our findings, as it was notably accounted for in the mixing models. Consequently, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of each group were pooled irrespectively to the section for further analyses. The temporal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in streams in summer is minimal (Závorka et al. 2017); therefore, baselines collected in June were also used for the analyses of YoY-age-0 trout collected in September.

### Statistical analyses

Possible differences in stable isotope niche between age classes, sections, or species were tested using MANOVA with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values as response variables and with age, section, or species and their interaction as independent variables. ANOVA was used to test possible differences in single stable isotope (i.e.,  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ) values. Trophic positions of each age class of each species in each study section were calculated using the package *tRophicPosition* (Quezada-Romegialli et al. 2018). Isotope niche size was then quantified using Bayesian standard ellipses  $\text{SEA}_b$  calculated for each age class of each species in each study section using R package SIBER version 2.1.3 (Jackson et al. 2011). The values of  $\text{SEA}_b$  were estimated based on the Bayesian methodology and account for 95% of variability in posterior distributions (Jackson et al. 2011). Overlap of  $\text{SEA}_b$  (percentage of sympatric brown trout stable isotope niche overlapping with sympatric brook trout stable isotope niche for each age class) and distance between centroids (CD; providing additional information on niche width, but also spac-

**Table 2.** Stable isotope niche size ( $SEA_b$ , mean and 95% CI), stable isotope niche overlap (mean and 95% CI) between sympatric brown trout and sympatric brook trout, and distances between the  $SEA_b$  ellipses centroids for allopatric brown trout (ST-all), sympatric brown trout (ST-sym), and sympatric brook trout (SF-sym) across the four age classes.

Age class	$SEA_b$ and sample size			$SEA_b$ overlap		Distance between centroids	
	ST-all	ST-sym	SF-sym	ST-sym-SF-sym	ST-sym-ST-all	ST-sym-SF-sym	ST-all-SF-sym
YoY-age-0	1.34 (1.31; 1.36) n = 13	1.08 (1.06; 1.10) n = 13	0.83 (0.79; 0.87) n = 4	20.37 (19.26; 21.49)	1.49	0.32	1.17
Parr-age-1	1.40 (1.38; 1.43) n = 17	1.54 (1.51; 1.56) n = 17	0.91 (0.90; 0.93) n = 17	24.88 (23.84; 25.92)	1.75	0.71	2.45
Parr-age-2	0.65 (0.64; 0.66) n = 20	1.94 (1.91; 1.97) n = 18	2.33 (2.29; 2.36) n = 20	5.27 (4.65; 5.89)	1.45	1.48	2.87
Adult-age-3+	1.58 (1.55; 1.61) n = 13	0.88 (0.87; 0.90) n = 15	1.42 (1.40; 1.44) n = 13	15.29 (14.13; 16.45)	1.59	1.21	2.79

ing between focal groups; Layman et al. 2007) were obtained using SIBER.  $SEA_b$  is unbiased with respect to sample size but exhibits more uncertainty with smaller sample size. Typically, sample sizes < 10 individuals can result in an underestimation of the population niche size. For YoY brook trout, we were able to collect samples only from four individuals (Table 2); therefore, overlaps between  $SEA_b$  involving this group might be underestimated, but this does not apply for CD between groups. Bayesian mixing models (SIAR; Parnell et al. 2010) were also 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. We used a general enrichment factor for both brown and brook trout (mean  $\pm$  SD:  $0.39 \pm 1.3$  and  $3.4 \pm 0.98$  for  $\delta^{13}C$  and  $\delta^{15}N$ , respectively; Post 2002). Differences in brown trout body condition was tested using ANOVA with age, study section, and their interaction as independent variables. Statistical analyses were performed using R 3.2.3 (R Core Team, Vienna, Austria).

## Results

When comparing sympatric with allopatric brown trout, we found a significant difference in the stable isotope niche of native brown trout between age classes ( $F_{[6,242]} = 30.97$ ;  $p < 0.001$ ) and allopatric and sympatric stream stretches ( $F_{[2,120]} = 65.74$ ;  $p < 0.001$ ; Fig. 1). The interaction between age classes and stream stretches was not significant ( $F_{[6,236]} = 0.529$ ;  $p = 0.786$ ). The difference in the stable isotope niche between age classes of native brown trout was driven by increasing  $\delta^{15}N$  ( $F_{[1,121]} = 40.95$ ;  $p < 0.001$ ) and  $\delta^{13}C$  ( $F_{[1,121]} = 39.94$ ;  $p < 0.001$ ) values with age (Fig. 1). This indicated that, independently on the coexistence with non-native brook trout, brown trout increased its trophic position during ontogeny. Overall, the difference in the stable isotope niche between the sections was driven by significantly lower  $\delta^{13}C$  values of brown trout in the sympatric section compared with the allopatric section ( $F_{[1,121]} = 129.337$ ;  $p < 0.001$ ; Fig. 1). There was, however, no significant difference in  $\delta^{15}N$  values of brown trout between the sympatric and allopatric sections ( $F_{[1,121]} = 1.451$ ;  $p = 0.2307$ ; Fig. 1). This suggests that although the trophic position of sympatric and allopatric brown trout was overall similar (Fig. 2), all age classes of brown trout consumed more terrestrial prey in sympatry with brook trout (mean  $\pm$  SD contribution of terrestrial prey to the diet of allopatric brown trout:  $10\% \pm 9\%$ ; sympatric brown trout:  $21\% \pm 14\%$ ; and sympatric brook trout:  $28\% \pm 15\%$ ; Fig. 3). Consequently, the shift of sympatric brown trout for higher consumption of terrestrial prey lead to an increased similarity with the diet of non-native brook trout (Fig. 3).

When comparing sympatric brown trout with sympatric brook trout, we found that the stable isotope niche overlap between the two species significantly changed across age classes ( $F_{[6,218]} = 3.282$ ;  $p = 0.004$ ; Fig. 1) and that these changes were caused by differences in  $\delta^{13}C$  ( $F_{[3,109]} = 4.7316$ ;  $p = 0.004$ ) but not in  $\delta^{15}N$  ( $F_{[3,109]} = 0.9614$ ;  $p = 0.414$ ) values (Fig. 1).  $SEA_b$  indicated that niche overlap was the

**Fig. 2.** Estimated trophic positions (mean and 95% credibility interval) of each age class of each species in each study section.



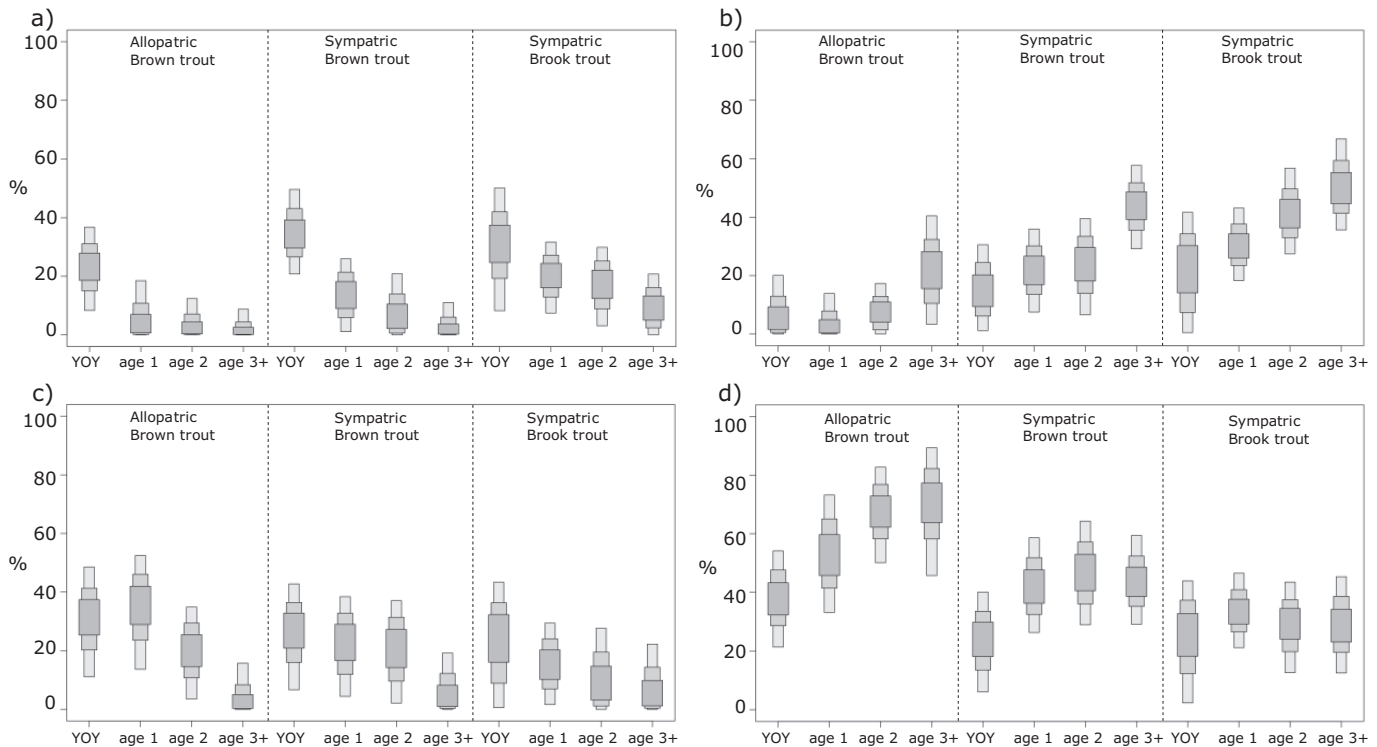
highest at the juvenile age classes (YoY-age-0 = 20.37% and parr-age-1 = 24.88%; Table 1; Fig. 4), and there was no significant difference in the  $\delta^{13}C$  values of brown and brook trout in sympatry for YoY-age-0 individuals ( $F_{[1,15]} = 0.409$ ;  $p = 0.532$ ; Fig. 4). Sympatric brown trout had significantly higher  $\delta^{13}C$  values than sympatric brook trout in all other age classes (parr-age-1:  $F_{[1,32]} = 10.246$ ;  $p = 0.003$ ; parr-age-2:  $F_{[1,36]} = 26.824$ ;  $p < 0.001$ ; adult-age-3+:  $F_{[1,26]} = 21.89$ ;  $p < 0.001$ ; Fig. 4), and there was lower niche overlap (5.27% and 15.29%, respectively) between sympatric brown and brook trout at the parr-age-2 and adult-age-3+ age classes than for the juveniles age classes (Table 2). These findings were confirmed by the distances between the centroids of the stable isotope niches (Fig. 4), which indicated that sympatric brown trout differed less from brook trout than from allopatric brown trout, especially at the youngest age classes (Table 2).

Finally, there was no significant effect of the section ( $F_{[1,192]} = 0.0017$ ;  $p = 0.9672$ ), the age class ( $F_{[3,192]} = 2.5828$ ;  $p = 0.054$ ), or their interaction ( $F_{[3,189]} = 0.2782$ ;  $p = 0.841$ ) on the body condition of brown trout.

## Discussion

Understanding the effects of coexistence with non-native species is crucial to improve our ability to predict and mitigate the ecological impacts of biological invasions. For example, the shift in diet composition of native species can reinforce the impact of invasion on ecosystem functioning through the trophic cascade (Des Roches et al. 2018). In such cases, the mitigation of the biological invasions might require additional effort to restore the native community structure after the invasive species eradication. In the present study, we found that, across most age classes, the stable isotope niche of sympatric brown trout was closer to

**Fig. 3.** Dietary contribution of (a) terrestrial herbivores, (b) terrestrial predators, (c) aquatic herbivores, and (d) aquatic predators across age classes of allopatric brown trout, sympatric brown trout, and sympatric brook trout. Proportions are calculated based on posterior distributions of probability densities estimated by SIAR Bayesian model. Credibility intervals displayed by the boxplots are 95% (dark grey), 75% (intermediate grey), and 25% (light grey).



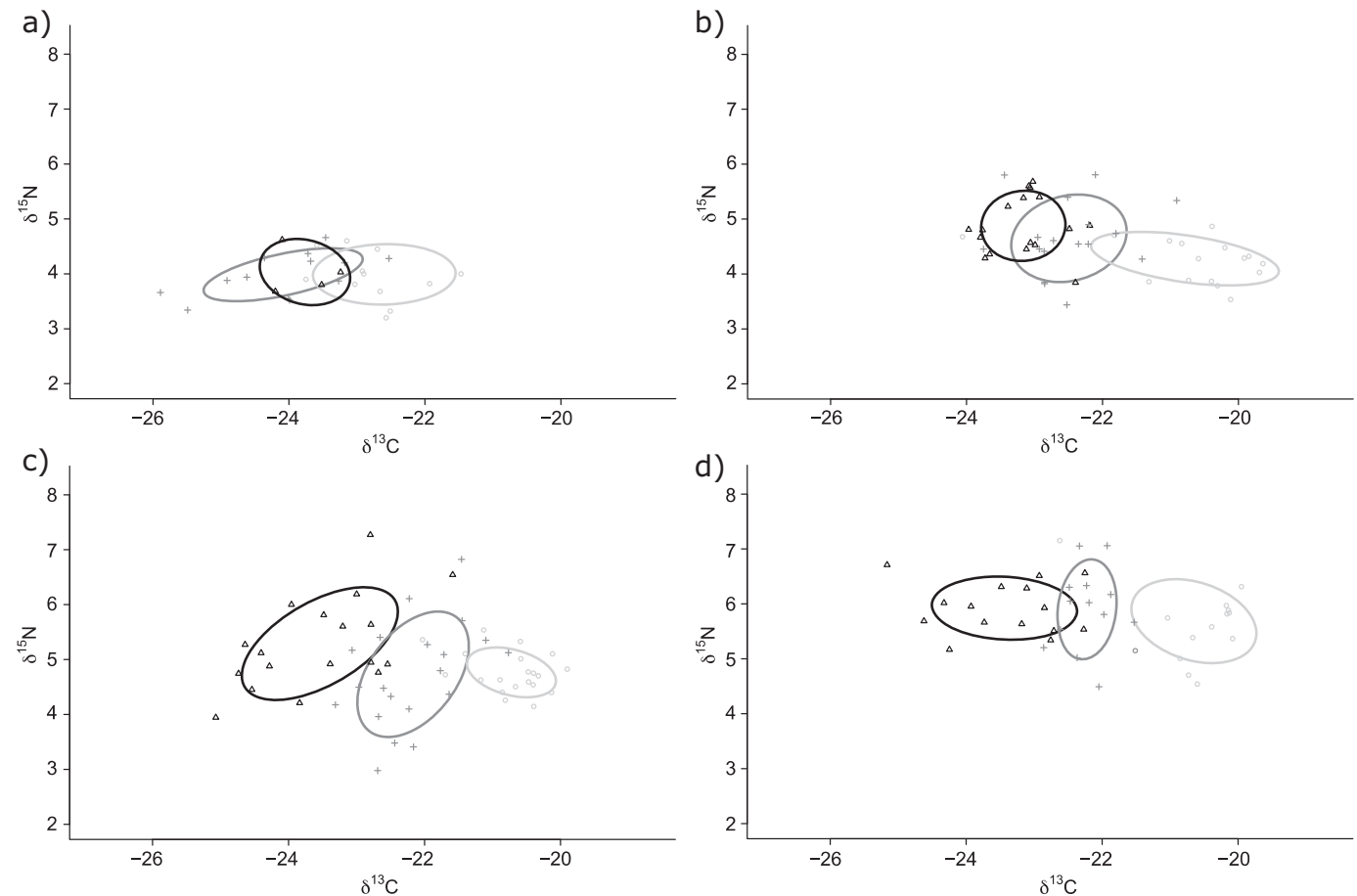
non-native brook trout than to the stable isotope niche of its conspecifics dwelling in allopatry, while the stable isotope niche of allopatric brown trout was clearly different from that of non-native brook trout across all age classes. The highest overlap of stable isotope niches between sympatric brown trout and brook trout occurred at the earliest age class of YoY (age-0) individuals and tended to decrease as individuals get older.

The comparison of diet inferred from stable isotope analyses indicates that brown trout consumes a higher proportion of terrestrial invertebrates when coexisting with non-native brook trout for all age classes. Specifically, terrestrial predators appeared to be much more common in diet of sympatric than allopatric brown trout. Terrestrial invertebrates have been reported to have ~20% higher energetic values than aquatic invertebrates (Cummins and Wuycheck 1971) but to contain a lower proportion of some essential micronutrients like polyunsaturated fatty acids (Guo et al. 2017), which are important for somatic development (Murray et al. 2014). We found that brown trout body condition was not significantly affected by the sympatry with non-native brook trout. This is in agreement with Blanchet et al. (2008), who demonstrated that native salmonid species could maintain their growth performances by compensating the energy spent when coexisting with the non-native species. Here, the consumption of more energetically rich terrestrial invertebrates by brown trout could compensate the energy costs of coexistence (e.g., territory defence) with non-native brook trout. Although this remains to be tested, the shift towards diet with suboptimal composition of micronutrients in native brown trout may have negative impacts on other phenotypic traits and their association (Öhlund et al. 2008; Závorka et al. 2017).

Composition and abundance of available prey did not differ across the study sites (Aymes 2005), and it is very unlikely that the temporal dynamics of food availability differed across sections. In addition, studied sites were relatively similar in terms of abiotic

characteristics, and it is very unlikely they could lead to diet convergence. Therefore, our results indicate that the differences of stable isotope niche between sympatric and allopatric brown trout might have been caused by a behavioural change of native brown trout exposed to the closely related non-native species. Previous studies suggested two plausible and nonexclusive behavioural mechanisms that might explain the higher consumption of terrestrial prey by sympatric brown trout. First, juvenile salmonids are known to aggressively interfere since their earliest age classes to defend profitable territories (Fausch 1984), and interactions between native and non-native salmonids could lead to increased activity during the daylight in the native species due to higher amount of aggressive interactions with the non-native species (Blanchet et al. 2008). A previous study demonstrated an increase of diurnal activity of sympatric brown trout caused by changes in territorial behaviour and aggressive interactions in the presence of non-native brook trout (Larranaga et al. 2019). Relative abundance of terrestrial prey in the drift is higher during the daylight (e.g., Aymes 2005); higher proportion of terrestrial prey in diet of sympatric brown trout could therefore be just a consequence of higher encounter rate of this prey type due to the change in diurnal activity pattern. Long-term studies on repeatability of individual differences in aggression and metabolic rates between allopatric and sympatric brown trout can provide further insight on this issue (Metcalf et al. 2016). The second mechanism could be a change of prey preference or foraging strategy by social learning. Social learning within, but also between, species has been repeatedly documented in fishes (Brown and Laland 2003; Coolen et al. 2003). It is possible that in the case of these two species, brown trout have learned to forage upon terrestrial prey from brook trout; in other words, they may have copied the feeding habits of brook trout in sympatric sections. Although the mechanism of information transfer between the two species remains to be tested, recent findings indicate that the patterns of

**Fig. 4.** Stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) SEA<sub>b</sub> ellipses for (a) young-of-the-year, (b) parr-age-1, (c) parr-age-2, and (d) adult-age-3+. SEA<sub>b</sub> ellipses for allopatric brown trout, sympatric brown trout, and sympatric brook trout are illustrated by light grey lines, dark grey lines, and black lines, respectively. Data points for individual trout are depicted by symbols corresponding to their section and species (allopatric brown trout = circles, sympatric brown trout = crosses, sympatric brook trout = triangles).



social interactions between the brown and brook trout are pre-adapted for interspecific social learning (Lovén Wallerius et al. 2017). Indeed, YoY brown trout does not distinguish between their conspecifics and non-native brook trout of the same age and tend to keep shorter distances from non-native brook trout than from conspecifics (Lovén Wallerius et al. 2017; Larranaga et al. 2019). Differences in the sampling period between YoY individuals and the other age classes are unlikely to affect our findings, and the seasonal variability in the intensity of the stable isotope niche convergence remains to be quantified.

The pre-existing ontogenetic differences in behaviour and ecology of native and non-native species may play an important role in determining the impacts of biological invasions (Langkilde et al. 2017). Niche divergence is generally thought to reduce competition and favour coexistence between species with overlapping niches (Connell 1980). Our study indicates that the interactions of coexisting native brown trout and non-native brook trout can induce niche convergence rather than divergence, which nevertheless seems to allow the long-term sympatric coexistence of both species. This is an illustration of the fact that when engaged into multiple interactions across generations, species may not necessarily interact in the direction predicted by competitive exclusion principle (Leibold and McPeck 2006). Understanding the mechanisms driving the stable isotope niche shift of juvenile native brown trout is now needed to fully appreciate the role of niche convergence in species coexistence.

## Acknowledgements

We thank all the people who contributed to fieldwork and the Office National de la Chasse et de la Faune Sauvage, the French Water Agency, and the Direction Régionale de l'Environnement for supporting this study (contract No. 2004/071617/N°1413467.00, ONCFS-FEDER). This study was also supported by the BiodivERSA-funded project SalmoInvade (ANR-13-EDIB-0002).

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