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Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator

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Summary

1. Many generalist populations are composed of specialized individuals that use a narrow part of the population's niche. Ecological theories predict that individual specialization and population trophic niche are determined by biotic interactions and resource diversity emerging from environmental variations (i.e. ecological opportunities). However, due to the paucity of empirical and experimental demonstrations, the genuine importance of each of these drivers in determining trophic niche attributes is not fully appreciated.

2. The present study aimed at determining the population level and individual responses of brown trout (*Salmo trutta*) to variations in ecological opportunities (terrestrial prey inputs) and autochthonous prey communities among 10 stream reaches along a riparian condition gradient using individual longitudinal monitoring and stable isotope analyses.

3. Our results suggested that trophic niche diversity varied along the environmental gradient, while individual trophic specialization was indirectly driven by ecological opportunities through strengthened intraspecific competition. Individual diet was repeatable over the study period, and the growth rate of juvenile brown trout increased with their specialization for aquatic predatory invertebrates.

4. Our findings highlight the dual influences of intraspecific competition and ecological opportunities on individual trophic specialization and population trophic niche.

Key-words: competition, individual performances, inter-individual variability, riparian land-use, stable isotope analyses, trophic subsidies

Introduction

Ecologists have long considered populations as a whole, neglecting traits variation among conspecific individuals and its significant ecological and evolutionary consequences (Bolnick *et al.* 2003). Morphological variations among individuals within populations are frequently related to niche differentiation through the use of different habitats and trophic resources to optimize foraging efficiency and subsequently increase individual performances (Bolnick *et al.* 2003; Svanbäck & Bolnick 2008; Cucherousset *et al.* 2011). However, in some cases, individuals within a population can exhibit different trophic niches and display slight (if no) morphological differences (Skúlason & Smith 1995; Tinker, Bentall & Estes 2008). This 'individual trophic specialization' is a widespread phenomenon (Bolnick *et al.* 2003), and a more comprehensive understanding of the mechanisms driving individual specialization is required (Araújo, Bolnick & Layman 2011).

Individual trophic specialization in wild populations has been mainly demonstrated to emerge from biotic interactions such as competition and predation (Svanbäck & Persson 2004; Eklöv & Svanbäck 2006; Bolnick *et al.* 2010). However, the relative contributions of competition and predation to individual trophic specialization are highly context dependent, and the degree of individual specialization may also depend on the diversity and/or availability of food resources. Ecological opportunities, that is, the resource diversity emerging from environmental variations (Araújo, Bolnick & Layman 2011), can

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*Correspondence author. E-mail: julien.cucherousset@univ-tlse3.fr strongly modify the occurrence and/or intensity of trophic specialization (Quevedo, Svanbäck & Eklöv 2009) but few studies have investigated this phenomenon in wild populations (e.g. Araújo, Bolnick & Layman 2011).

Trophic subsidies (i.e. spatial flows of food resources across ecosystem boundaries), by enhancing the availability, diversity, and/or temporal fluctuations of food resources, have the potential to promote individual trophic specialization (Araújo, Bolnick & Layman 2011). Optimal utilization of trophic subsidies often involves changes in foraging behaviour and habitat use of consumers in response to the spatial segregation of allochthonous and autochthonous resources. Studies on pulsed marine-derived resources, through the anadromous migration of spawning salmons, have shown that terrestrial predators foraging on these trophic subsidies are more specialized than individuals that are spatially restricted to forage uniquely on terrestrial prey (Darimont, Paquet & Reimchen 2009; Wipfli & Baxter 2010).

Trophic subsidies have been reported to mediate human impacts on ecosystems. For instance, commercial fisheries and habitat alteration have led to drastic declines in migratory salmonids stocks (Allendorf & Hard 2009) with subsequent consequences on the fluxes of marine-derived nutrients in freshwater ecosystems (Schindler *et al.* 2005). Invasive species can also modify the transfer of allochthonous energy in recipient ecosystem (Baxter *et al.* 2004), with some invasive individuals displaying trophic specialization for allochthonous prey (Cucherousset *et al.* 2012).

Across the stream–forest interface, allochthonous inputs, principally composed of nutrients, plant detritus and organisms are used by a wide range of consumers inhabiting the recipient ecosystem (Baxter, Fausch & Saunders 2005; Bartels *et al.* 2012). Previous studies have highlighted the importance of terrestrial invertebrates to the diet and annual energy budget of many stream fish (e.g. Kawaguchi & Nakano 2001; Baxter *et al.* 2007; Bartels *et al.* 2012). For instance, substantial inputs of terrestrial invertebrates from a productive forest ecosystem to a nutrient-poor stream can represent more than half of the energy requirement of stream fish in summer (Kawaguchi & Nakano 2001).

Riparian land-use and forest management alter the inputs of terrestrial invertebrate prey to streams (Nakano, Fausch & Kitano 1999a; Kawaguchi & Nakano 2001) and community of aquatic invertebrate prey (Kiffney, Richardson & Bull 2003; Lecerf *et al.* 2012). Terrestrial plant litter is the primary energy source to forested streams, and thus, loss of forest cover is expected to reduce the production of aquatic invertebrate detritivores (Wallace *et al.* 1997). Conversely, the production of aquatic invertebrate herbivores should increase with riparian canopy openness as in-stream primary producers (e.g. algae and moss) are released from light limitation (Kiffney, Richardson & Bull 2003). Riparian canopy cover also regulates stream temperatures (Moore, Spittlehouse & Story 2005) and, subsequently, the metabolism of aquatic organisms. As opportunistic predators, stream salmonids can shift their diet in response to quantitative and qualitative changes in terrestrial prey inputs and aquatic prey community to meet their nutritional requirements (Nakano, Miyasaka & Kuhara 1999b; Baxter *et al.* 2004), with potential modifications of population patterns of trophic specialization and individual performances. However, despite compelling evidence that salmonids are affected by forest management, little is known on the genuine importance of trophic factors in mediating individual- and population-level responses of fish to changes in riparian canopy cover (Mellina & Hinch 2009; Lecerf *et al.* 2012).

In the present study, we investigated the trophic ecology of brown trout (*Salmo trutta*), an opportunistic predator, in low-order streams flowing through a deciduous hardwood forest, using stable isotope analyses (Layman *et al.* 2012). Ten stream sites were selected along a gradient of riparian canopy cover in a forested area managed under traditional silvicultural systems, anticipating changes in the availability and the composition of aquatic and terrestrial prey along this environmental gradient. We quantified trophic specialization and trophic diversity of brown trout in each site. In addition, we determined individual diet and growth rate as a fitness proxy to infer possible ecological benefits of individual specialization (Bolnick 2004). We first predicted that terrestrial prey inputs are ecological opportunities for brown trout and increased under dense canopies. Then, we predicted that dense riparian canopy cover should promote individual trophic specialization and influence population trophic niche attributes in brown trout. In addition to the ecological opportunities hypothesis, we also evaluated the importance of intraspecific competition in mediating the brown trout response to variation in riparian canopy cover.

Materials and methods

STUDY AREA AND SITE SELECTION

The present study was conducted from April to September 2011 in the Montagne Noire (South-Western France; 43°33′N, 1°29′E), a low altitude mountain region drained by a high density of headwater streams. Catchments are historically covered by European beech (*Fagus sylvatica*) forest. During the twentieth century, upland forests were converted into commercial beech production and conifer plantations. Valley bottoms and riparian forest are still managed under traditional silvicultural systems. For instance, several areas comprise oak coppice-with-beech standards, where natural regenerating vegetation is preserved. A few areas are affected by riparian clear-cut logging. However, due to the small size of harvesting patches (< 5% of total catchment area) and the protection measures taken to minimize disturbance by logging machines, the ecological impact on stream ecosystems, other than those mediated by changes in riparian canopy structure and composition, was small (Lecerf *et al.* 2012).

Brown trout was the only fish species present in the study streams. To assess the effect of changes in forest canopy cover on its trophic ecology, we selected 10 stream sites representing a gradient of riparian canopy openness, an integrative metric to reveal the importance of riparian vegetation on aquatic ecosystem properties (Lecerf *et al.* 2012). Sites were situated on the lower third section of *c.* 500-m-long stream reaches running through homogeneous riparian vegetation in terms of canopy structure and species composition. Site length ranged from 55·4 to 96·0 m and was also selected to reduce potential confounding effects of stream habitat features on brown trout (Appendix S1, Supporting information). All sites were located on different streams with the exception of two sites that were considered, however, as independent observations because they were located 1·3 km apart. Mean canopy openness was quantified as canopy gap area within a 0–60° zenith range based on four digital hemispherical pictures taken from the streambed in early summer 2011 at fully foliated stage (Lecerf *et al.* 2012). Image analyses were performed using the software 'Gap Light Analyzer v 2.0' (Simon Fraser University, Canada). Differences in riparian forest canopy openness were due to variable forest management intensity (coppicing or partial harvesting), forest age and natural determinants of canopy structure (i.e. forest blowdown, soil properties and topography). The most open sites were selected in young (5–10 year old) forests regenerating from clear-cutting. Canopy gaps represented < 1% of sky surface at the least open site and reached nearly 50% at the most open site. The remaining eight stream sites were rather evenly distributed over the range of canopy openness despite a gap in the 8·6–18·6% range (Table S1, Supporting information). Canopy openness was significantly different between sites (ANOVA, $F_{9,30} = 39$, $P < 0{\cdot}001$), and within-site variability measured on four pictures was low (residual variance accounted for 8% of total variance).

HABITAT CHARACTERISTICS AND TROPHIC RESOURCES AVAILABILITY

Water temperature was recorded automatically from March 2011 to September 2011 every two hours using HOBO Pendant® Temperature loggers (Onset company, Cape Cod, MA, USA) anchored to an iron stick placed in the downstream part of each study site. Channel width was determined using transects set every 10 m along each site in spring 2012. Water depth was determined at three equally spaced points along each transect. The proportion of riffle and pool habitats occurring between transects was visually determined to estimate per cent wet area covered by each habitat.

Aquatic prey availability was quantified by estimating benthic invertebrate biomass on the 21 June 2011–23 June 2011, that is, during the period of fish monitoring (*see details below*) and of maximal benthic invertebrate abundance. Surber samples (25 × 25 cm; 250-μm mesh size) were randomly taken in riffle ($n = 4$) and pool ($n = 4$) habitats in each site. The flux of terrestrial prey falling into the streams was estimated using three plastic pan-traps (55 × 37 cm; 15 cm deep) deployed along the stream banks of each site on the 1 August 2011, when terrestrial invertebrate falling into stream peaked and weather conditions were stable. This sampling effort (mean = 0·04 pan-trap per metre) falls within a range of sampling effort reported in the literature (Kawaguchi & Nakano 2001; Nakano & Murakami 2001). Pan-traps were filled with filtered water, and 2–3 drops of surfactant were added. After 48 h of deployment, water in pan-traps was sieved at 250 μm to collect invertebrates. Aquatic and terrestrial invertebrate samples were preserved in 70% ethanol and stored at 15 °C until processing. In the laboratory, invertebrates were counted and sorted to the lowest practical level (mostly genera or family) under a binocular microscope (magnification × 80). Aquatic invertebrates were assigned to the trophic groups of aquatic predators, aquatic herbivores or aquatic detritivores using literature information on feeding habits and food preference (Tachet *et al.* 2010). Adult aquatic insects were removed from pan-trap samples, and remaining invertebrates were assigned to the trophic groups of terrestrial predators or terrestrial herbivores. The habitat-weighted biomass of aquatic prey per square metre was then calculated based on the number of individuals of each trophic group in riffle and pool habitats, the average individual dry mass and the proportion of each habitat type. Larvae, nymph and imagos of each taxon had distinct weights and were considered separately. After identification, terrestrial prey were oven-dried at 60 °C for 48 h and weighed to the nearest 0·01 mg for total dry mass. The daily flux of terrestrial prey per trophic group was calculated using dry mass, pan-trap surface and trapping duration.

FISH MONITORING AND SAMPLES ANALYSES

Fish were initially captured and individually tagged from the 18th to 20th of April 2011 using two-path electric fishing (EFKO FEG 1500, Leutkirch im Allgäu, Germany) in study sites delineated with two 8-mm-mesh nets prior to sampling. Fish were anesthetized, measured for fork length ($\mathrm{FL_C} \pm 1$ mm) and weighed ($W_\mathrm{C} \pm 0{\cdot}1$ g). For each individual, we collected scales for age determination and a tissue sample from the left pelvic fin, which was stored on ice and frozen for stable isotope analyses (Appendix S2, Supporting information). Stomach contents of individuals with $\mathrm{FL_C} > 65$ mm were collected by stomach flushing using a pumping method (e.g. Nakano, Miyasaka & Kuhara 1999b) and stored in 70% ethanol. Individuals with $\mathrm{FL_C} > 50$ mm were tagged using fluorescent visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, WA, USA). Because the coding was based on a limited number of colour combinations ($n = 2$), body location ($n = 7$) and number of tags (1 or 2), there was a lack of unique tags compared with the number of fish in a few sites and, consequently, some individuals were only fin-clipped. Lastly, individuals were placed in well-oxygenated water and released back into the capture site after their full-recovery. A total of 249 brown trout were captured, among which 195 were individually tagged.

Five months later (from 12th to 14th September 2011), recaptures were carried out using the same sampling method and a total of 446 brown trout were captured. After anaesthesia, all individuals were checked for evidence of recapture. Recaptured individuals were measured ($\mathrm{FL_R} \pm 1$ mm), weighed ($W_\mathrm{R} \pm 0{\cdot}1$ g), fin-clipped, and stomach contents were collected. The same procedure was applied to unrecaptured individuals, and scales were also collected for age determination. Young-of-the-year juveniles that hatched in April 2011–May 2011 (i.e. during the monitoring) were rarely present and were consequently not considered in subsequent analyses. For individuals that were recaptured fin-clipped in September but not VIE-tagged in April, 'individual genetic tagging' was carried out using subsamples of fin preserved in 70% ethanol and nine microsatellite loci (see methodological details in Andreou *et al.* 2012). After DNA extraction, PCR amplifications were run and allelic sizes (two allele per loci) were scored using GeneMapper 4.0 (Applied Biosystems, Foster City, CA, USA). Recaptured individuals were subsequently reassigned to capture individuals using individual genotypes and FL_C (Andreou *et al.* 2012). Among the 446 brown trout captured, 93 were tagged in spring, leading to a 47·7% recapture rate. Although salmonids could be relatively mobile (Gowan *et al.* 1994), we focused our analyses at the individual level on recaptured individuals only.

To quantify trophic specialization following Araújo *et al.* (2007), prey items from stomach contents were counted, identified and assigned to trophic groups as described above. Fish diet was found to be exclusively composed of terrestrial and aquatic invertebrates, with no evidence of cannibalism. The dietary contribution of each prey taxon to individual fish was estimated by the product of prey number by the average oven-dried (60 °C for 48 h) mass determined on 2–40 intact prey weighed to the nearest 0·1 mg (e.g. Araújo *et al.* 2007). Stable isotope analyses were performed on fin samples of all recaptured individuals for each sampling period. When possible, additional fish collected in September were analysed to reach a minimum of 15 individuals per site. Therefore, stable isotope analyses were performed on all recaptured individuals (93 individuals with two samples per individual), and 111 additional individuals only sampled in September (Appendix S2, Supporting information). Additionally, potential prey were collected for stable isotope analyses in each studied site during fish sampling (April and September). Prey were collected according to their abundance, and samples for stable isotope analyses were composed of pooled items to account for potential spatial variability within site (n = 3–30 individuals per sample; e.g. Cucherousset *et al.* 2011). Prey were categorized into five trophic groups: aquatic herbivores, aquatic predators, aquatic detritivores, terrestrial herbivores and terrestrial predators (further details available in Appendix S2, Supporting information). Within-group variability in stable isotope values was low compared with between-group variability (Appendix S2, Supporting information), and therefore, these five functional and isotopic groups were used for subsequent analyses.

QUANTIFICATION OF TROPHIC SPECIALIZATION, TROPHIC DIVERSITY AND TROPHIC NICHE

Trophic specialization was calculated using the integrative method developed by Araújo *et al.* (2007). This approach is based on the dietary proportion of each prey group determined from stomach contents, their $\delta^{13}C$ value and their dry mass to calculate an index of individual trophic specialization, $IS_{(exp)}$, using the relationship between expected isotopic variance and individual trophic specialization (details available in Araújo *et al.* 2007). The calculations were performed using the program 'Var-Iso' with 5700 simulations (Araújo *et al.* 2007). For the sake of clarity, we used the 'index of specialization' ($1-IS_{(exp)}$). Values closer to 1 indicated higher degree of trophic specialization in the population (Bolnick *et al.* 2002).

Trophic diversity in each population was quantified using stable isotope values (Layman *et al.* 2007) with 'Stable Isotope Bayesian Ellipse in R', an approach developed to cope with disparities in sample size and to incorporate uncertainty in stable isotope values (Jackson *et al.* 2011). Although the number of individuals sampled in each population was representative of population size, this ellipse-based method focused on the core of the isotopic niche represented by the standard ellipse area (SEA). Population trophic diversity was estimated using SEA_b, the Bayesian estimate of the SEA that was calculated using 10 000 replicates (Jackson *et al.* 2011).

To determine the trophic niche at the individual level, Bayesian mixing model SIAR (Parnell *et al.* 2010) was used to quantify the relative dietary contribution (%) of each trophic group of prey assimilated by consumers (Layman *et al.* 2012). SIAR allows the integration of variability in prey and consumer stable isotope values, trophic enrichment factors and other unquantifiable sources of uncertainty. As the C : N ratio of invertebrates was high, their stable isotope values were lipid corrected (Post *et al.* 2007; details available in Appendix S2, Supporting information). As there is no specific trophic enrichment factors for the model species reported in the literature, we followed a conservative approach and used trophic enrichment factors of 1·0‰ (± 1·0 SD) and 3·3‰ (± 1·0 SD) for $\delta^{13}C$ and $\delta^{15}N$, respectively (e.g. Cucherousset *et al.* 2011). Models were run separately at tagging using stable isotope values of prey sampled in April (analytical precision used as a variation estimated) and at recapture using the mean and standard deviation of prey sampled in April and September. This was performed to incorporate potential temporal variability of prey stable isotope values over the study period and to match with consumer tissue turnover (Layman *et al.* 2012).

STATISTICAL ANALYSES

Results from a previous study (Lecerf *et al.* 2012) and visual examination of our data suggested that stream ecosystem responses to canopy openness may be nonlinear. A linear model with a quadratic term was thus used to assess monotonic (linear and nonlinear) and non-monotonic (hump-shaped and U-shaped) relationships between canopy openness and the response variables (i.e. trophic resource availability, brown trout densities, specialization and trophic diversity) determined at the site level (n = 10). To guard against overfitting, the quadratic term was removed for models when not significant ($P > 0{\cdot}05$; Crawley 2007). Canopy openness was square-root transformed to ensure more even dispersion of sites along the gradient. When needed, response variables were transformed to meet the assumptions of linear models. Specifically, brown trout densities and trophic diversity were log transformed.

Trout population densities (ind. 100 m^{-2}) in stream sites were estimated based on data collected on the second sampling date (September). Statistics were conducted on brown trout population densities, densities of age-1 individuals and densities of > age-1 individuals only (i.e. 'population density', 'juvenile density' and 'adult density', respectively) to assess if age class with the greatest nutritional demand would respond the most to change in canopy cover and prey availability. Linear models were used to test the effects of the inputs of allochthonous prey on brown trout density and to test the potential effects of brown trout density (i.e. 'population density') on trophic specialization and trophic diversity.

To determine individual responses to canopy openness, we first tested the existence of temporal maintenance of individual trophic specialization using a repeatability approach of the dietary contribution of aquatic predators and terrestrial predators obtained from individual mixing models. Terrestrial and aquatic predators were selected because of their high contribution to trout diet over the study period (see Results). Adjusted repeatability was quantified using the intra-class correlation coefficient (ICC) given by linear mixed models (LMM) with individual identity as a random factor (Nakagawa & Schielzeth 2010).

Individuals with only one measurement (i.e. individuals tagged in April but not recaptured and untagged individuals captured in September) were also included in the models (Kluen & Brommer 2013), and site was used as a fixed effect (Nakagawa & Schielzeth 2010). Then, individual growth rate was used as integrative proxy of individual performances (Cucherousset *et al.* 2011). Growth rate of recaptured individuals (% month^{-1}) was calculated using: Growth rate = $100 \times (\ln W_R - \ln W_C)$/(number of months). The effects of trophic niche specialization on fish growth rate were then tested using LMM with site as a random factor (Pinheiro *et al.* 2012). Fixed effects were canopy openness modelled as linear and quadratic terms to assess between-site differences, brown trout population density and age class (i.e. juveniles vs. adults to account for the fact that fish growth is not isometric) and dietary contribution of selected prey groups as indicator of individual trophic specialization within populations. The full model also included the interaction between age and individual trophic niche to assess age-specific response of individual performances to specialization. The interaction was removed from the model when it was not significant (Crawley 2007). All statistical analyses were performed using R (R Development Core Team 2011).

Results

HABITAT CHARACTERISTICS AND PREY RESPONSE TO CANOPY OPENNESS

The 10 streams had narrow channels (mean wet channel width: 1·6–3·9 m) with shallow water (mean water depth: 12–20 cm). Riffles were consistently the dominant habitat type (per cent channel area: 54·4–94·4%, Appendix S1, Supporting information). Stream sites differed in mean (March to September 2011) and maximum (July–August) water temperature, but these variations were not significantly related to canopy openness ($R^2 = 0{\cdot}26$, $P = 0{\cdot}126$ and $R^2 = 0{\cdot}18$, $P = 0{\cdot}229$, respectively). Importantly, stream sites differed substantially in the availability of aquatic (Fig. 1a) and terrestrial (Fig. 1b) invertebrate prey. Although a general increase was observed, the relationship between canopy openness and the total biomass of aquatic prey was not significant ($R^2 = 0{\cdot}29$, $P = 0{\cdot}112$). In fact, canopy openness strongly determined the biomass of aquatic herbivores that increased substantially and linearly with canopy openness ($R^2 = 0{\cdot}73$, $P = 0{\cdot}002$; Fig. 1c). No significant relationships between canopy openness, biomass of aquatic detritivores and aquatic predators were observed ($R^2 < 0{\cdot}01$, $P = 0{\cdot}948$ and $R^2 = 0{\cdot}05$, $P = 0{\cdot}552$, respectively), showing no predictable responses of these prey categories to canopy openness. Differences in canopy openness explained significantly the inputs of terrestrial prey that followed a U-shaped curve with the lowest inputs of allochthonous prey measured at the sites with intermediate levels of canopy openness ($R^2 = 0{\cdot}64$, linear term: $P = 0{\cdot}010$, quadratic term $P = 0{\cdot}009$; Fig. 1b). This trend was determined by the inputs of terrestrial herbivores ($R^2 = 0{\cdot}55$, linear term: $P = 0{\cdot}024$, quadratic term: $P = 0{\cdot}030$) rather than terrestrial predators ($R^2 = 0{\cdot}22$, $P = 0{\cdot}171$; Fig. 1d).

POPULATION RESPONSES TO CANOPY OPENNESS

The population density of brown trout in late summer ranged from 7·3 to 37·5 ind. 100 m^{-2} and was not significantly related to canopy openness ($R^2 = 0{\cdot}07$, $P = 0{\cdot}481$; Fig. 2a). Juvenile density varied over a 23-fold range, and the proportion of juveniles in populations ranged from 4 to 94%. Juvenile density showed a U-shaped curve response to canopy openness ($R^2 = 0{\cdot}52$, linear term: $P = 0{\cdot}079$, quadratic term: $P = 0{\cdot}049$; Fig. 2a), while no significant relationship was found for the density of adults ($R^2 = 0{\cdot}01$, $P = 0{\cdot}745$). In addition, no significant relationship between population density of brown trout and the input of allochthonous prey was observed ($R^2 = 0{\cdot}21$, $P = 0{\cdot}148$; Fig. 2b), but juvenile density was positively affected by the input of allochthonous prey ($R^2 = 0{\cdot}42$, $P = 0{\cdot}043$; Fig. 2b).

Population trophic specialization varied over a 4-fold range [from 0·14 (95% CI: 0·08–0·21) to 0·50 (95% CI: 0·45–0·69)] but was not significantly associated with canopy openness ($R^2 = 0{\cdot}32$, $P = 0{\cdot}090$; Fig. 2c, Table 1). The level of ecological opportunities did not explain variation in trophic specialization as no significant relationship between the inputs of terrestrial prey and trophic specialization at the population level was detected ($R^2 = 0{\cdot}03$, $P = 0{\cdot}642$). In contrast, trophic specialization was explained by population density ($R^2 = 0{\cdot}68$, linear term: $P = 0{\cdot}033$, quadratic term: $P = 0{\cdot}024$; Table 1). Specialization slightly decreased among the eight sites with smallest trout population (mean index = 0·22), and it increased substantially in the two sites with the largest populations (Fig. 2d).

Trophic diversity of brown trout population was highly variable across sites [from 0·81 (95% CI: 0·50–1·14) to 4·34 ‰^{2} (95% CI: 2·96–5·72)] and was tightly related to canopy openness in a non-monotonic manner ($R^2 = 0{\cdot}72$, linear term: $P = 0{\cdot}005$, quadratic term: $P = 0{\cdot}009$; Table 1). The hump-shaped curve indicated that trophic diversity was the highest at intermediate levels of canopy openness (Fig. 3a). In contrast, no significant relationship between trophic diversity and brown trout population density was observed ($R^2 < 0{\cdot}01$, $P = 0{\cdot}962$; Fig. 3b, Table 1).

INDIVIDUAL CONSEQUENCES

Mixing models predicted that terrestrial and aquatic predators were, overall, the main prey consumed by brown trout (i.e. mean = 26·4% (± 0·06 SD) and 22·1% (± 0·05 SD), respectively). The dietary contribution of terrestrial and aquatic predators to the diet of each recaptured individual was significantly repeatable between spring and late summer (ICC = 0·49, $P < 0{\cdot}001$ and ICC = 0·51, $P < 0{\cdot}001$, respectively, $n = 319$), indicating that individuals were specialized. The consumption of terrestrial predators had no significant effect on individual growth rate ($P = 0{\cdot}225$; Table 2), while a higher dietary

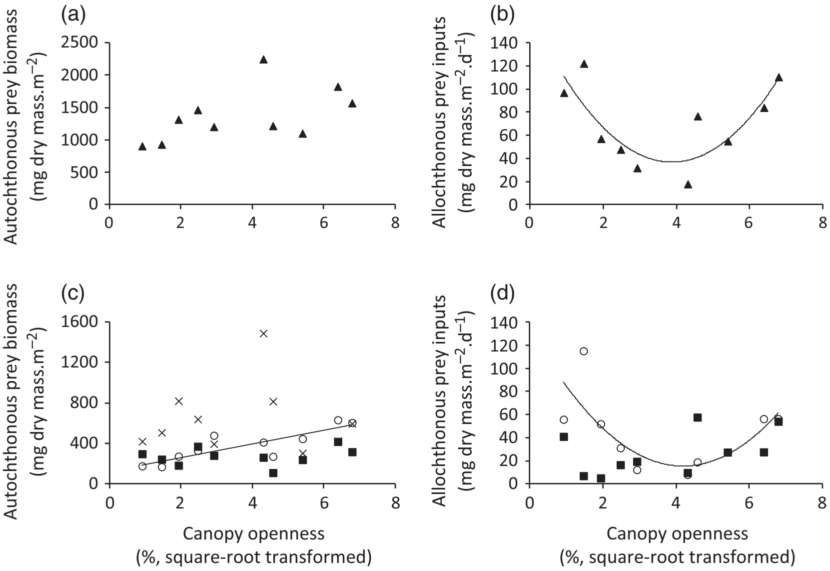

Fig. 1. Relationship between canopy openness (%, square-root transformed) and (a) the biomass of autochthonous prey (mg dry mass m^{-2}), (b) the inputs of allochthonous prey (mg dry mass m^{-2} day^{-1}), (c) the biomass of aquatic predators, herbivores and detritivores (solid squares, open dots and crosses, respectively, in mg dry mass m^{-2}), and (d) the inputs of terrestrial predators and herbivores (solid square and open dots, respectively, mg dry mass m^{-2} day^{-1}) in the 10 stream sites. Significant relationships are depicted using continuous lines.

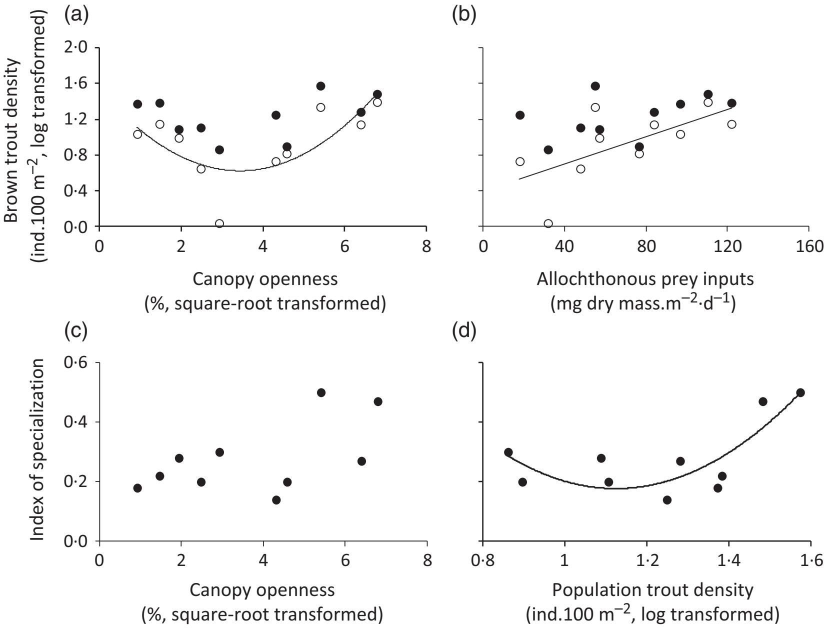

Fig. 2. Relationship between (a) canopy openness (%, square-root transformed) and (b) the inputs of allochthonous prey (mg dry mass m^{-2} day^{-1}) and the population (solid symbols) and juvenile (open symbols) density (ind. 100 m^{-2}, log transformed) of brown trout in the 10 stream sites. Relationship between (c) canopy openness (%, square-root transformed) and (d) the population density (ind. 100 m^{-2}, log transformed) of brown trout and the index of specialization in the 10 stream sites. Significant relationships are depicted using continuous lines.

contribution of aquatic predators was associated with a higher growth rate ($P < 0{\cdot}001$; Table 2). This effect was, however, age-dependent (interaction term: $P = 0{\cdot}002$; Table 2; Appendix S1, Fig. S1, Supporting Information), and juvenile brown trout displayed a stronger growth advantage than adults. Canopy openness had no significant effect on individual growth rate ($P > 0{\cdot}866$; Table 2).

Discussion

The ecological importance of trophic subsidies between riparian forest and aquatic ecosystems has now been widely recognized, including their role in consumer–prey dynamics and their direct effects on consumers (e.g. Baxter, Fausch & Saunders 2005; Bartels *et al.* 2012). The

Table 1. Results of the simplified regression models assessing linear and quadratic relationships between canopy openness and brown trout population density and trophic specialization and trophic diversity (n = 10)

Response variables	Source of variation	d.f.	Estimate (SE)	*t*	*P*
Trophic specialization	Canopy openness	8	0·03 (0·02)	1·93	0·090
	Intercept	8	0·15 (0·07)	2·17	0·062
Trophic diversity	Canopy openness	7	0·43 (0·11)	3·97	**0·005**
	Canopy openness^2	7	−0·05 (0·01)	−3·59	**0·009**
	Intercept	7	−0·54 (0·18)	−3·05	**0·018**
Trophic specialization	Density	7	−3·41 (1·29)	−2·64	**0·033**
	Density^2	7	1·50 (0·52)	2·86	**0·024**
	Intercept	7	2·13 (0·78)	2·74	**0·029**
Trophic diversity	Density	8	−0·02 (0·33)	−0·05	0·962
	Intercept	8	0·21 (0·41)	0·50	0·632

Significant *P*-values are displayed in bold.

summer input of terrestrial prey to streams represents an ecological opportunity for opportunistic predators, such as brown trout, that have high-energy requirements during warmer months of the year. This idea is supported by a large body of literature on the trophic ecology of salmonids (Kawaguchi & Nakano 2001; Nakano & Murakami 2001) and by the positive relationship between allochthonous prey inputs and juveniles density measured in the present study. In addition, we provide evidence that riparian land-use and forest management may affect the population patterns of trophic specialization and individual performances in brown trout (Fig. 4). Changes in ecological opportunities, by directly affecting the density of consumers, may indirectly modify the degree of individual specialization. Individual longitudinal monitoring (Araújo, Bolnick & Layman 2011) further indicates that individual diet variability on most of the functionally important prey was repeatable over the growing season, having subsequent effects on individual performances (Fig. 4).

Previous studies on the effects of riparian forest cover on trophic subsidies have mainly hinted at the linear decline of allochthonous prey inputs with riparian forest alteration (e.g. Kawaguchi & Nakano 2001; Baxter *et al.* 2004; Erős *et al.* 2012). As the present study was based on forest streams along a gradient of canopy openness rather than a comparison between extreme cases, we were able to detect nonlinear changes in allochthonous prey inputs (Fig. 4). Although counterintuitive, the rise of terrestrial invertebrate inputs along the second half of the gradient could be explained by the growth of understorey vegetation as canopy opening enhances ground luminosity

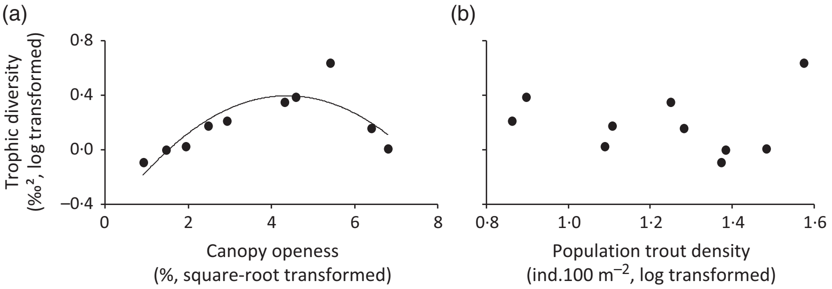

Fig. 3. Relationship between (a) canopy openness (%, square-root transformed) and (b) population density of brown trout (ind. 100 m^{-2}, log transformed) and trophic diversity (‰^{2}, log transformed) in the 10 studied populations. The significant relationship is depicted using continuous line.

Table 2. Results of linear mixed models used to test for both the effects of canopy openness and individual trophic specialization [dietary contribution of aquatic (Model 1) or terrestrial (Model 2) predators] on growth rate of recaptured individuals

Model	Source of variation	d.f.	Estimate (SE)	*t*	*P*
Model 1	Age (juveniles vs. adults)	1,81	−7·36 (0·98)	−7·52	**< 0·001**
	Terrestrial predators	1,81	−11·19 (9·16)	−1·22	0·225
	Canopy openness	1,7	0·03 (0·57)	0·05	0·963
	Population density	1,7	−2·30 (5·14)	−0·45	0·669
	Intercept	1,81	18·29 (6·55)	2·79	**0·007**
Model 2	Age (juveniles vs. adults)	1,80	9·34 (5·19)	1·80	0·076
	Aquatic predators	1,80	64·66 (10·08)	3·58	**< 0·001**
	Canopy openness	1,7	0·08 (0·43)	0·18	0·866
	Population density	1,7	−1·49 (4·02)	−0·37	0·722
	Age*Aquatic predators	1,80	−69·09 (21·45)	−3·22	**0·002**
	Intercept	1,80	−1·50 (7·06)	−0·21	0·832

Significant *P*-values are displayed in bold.

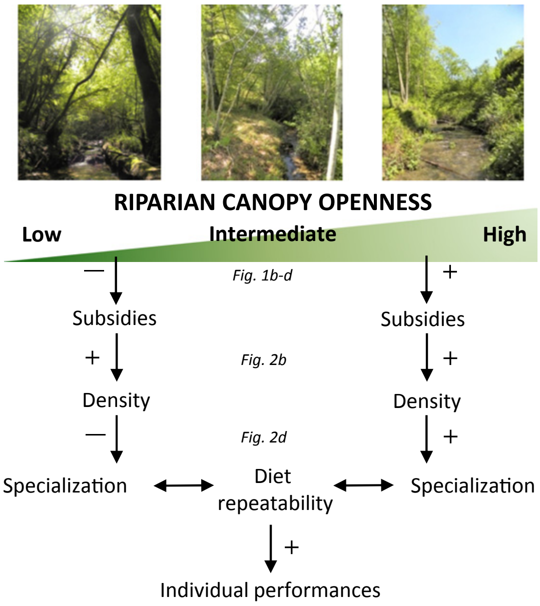

Fig. 4. Synthetic representation of the effects of changes in riparian canopy openness caused by human activities on trophic subsidies and subsequent consequences on brown trout (i.e. density, specialization and performances).

(Basset *et al.* 2001), thereby increasing the abundance of ground terrestrial invertebrates. As a consequence, a U-shaped relationship between juvenile brown trout density and canopy openness was observed (e.g. Lecerf *et al.* 2012), indicating that ecological opportunities can lead to an increase population density.

Trophic specialization and terrestrial prey inputs were not related, suggesting that factors other than resource diversity and availability may have prevailed in determining brown trout individual specialization in our study. Intraspecific competition is often cited as a key determinant of individual specialization (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Tinker, Bentall & Estes 2008; Svanbäck *et al.* 2011) because competition favours resource partitioning and thus increases diet variation within a population (Araújo, Bolnick & Layman 2011). Here, the intraspecific competition hypothesis is supported by the maximum degree of individual specialization reached in the populations with the highest densities.

Dispersion of individuals in the isotopic niche space depicts the degree of population trophic diversity (Layman *et al.* 2007*;* Jackson *et al.* 2011). It peaked at intermediate sites possibly because terrestrial prey inputs are lowest, suggesting that brown trout predation was mainly directed towards different aquatic prey. Moreover, aquatic prey in these streams displayed a wide range of carbon isotope values (Appendix S2, Supporting information), potentially leading to an increased trophic diversity of brown trout. Aquatic invertebrates rely on mixed carbon sources with distinct isotopic signatures; terrestrial plant litter being ^{13}C-depleted, and autochthonous primary producers (algae, moss) being ^{13}C-enriched (Hoeinghaus & Zeug 2008). Although terrestrial plant litter is the primary energy source to forested streams (Wallace *et al.* 1997), its contribution to secondary production may decrease as in-stream autochthonous production increases in response to riparian canopy opening (Kiffney, Richardson & Bull 2003; England & Rosemond 2004). Autochthonous and allochthonous carbon sources should therefore contribute more equitably to stream food webs at intermediate canopy cover.

Multiple samples from the same individuals using individual tagging and stable isotope analyses (e.g. Cunjak *et al.* 2005; Cucherousset, Paillisson & Roussel 2013) indicated that individual diet was strongly repeatable over several months during the growth season and increased individual performance in our study. Optimal foraging theory predicts that consumer selects their prey to maximize energy acquisition which, in turn, should improve individual performances (e.g. Svanbäck & Bolnick 2008; Bolnick & Araújo 2011; Cucherousset *et al.* 2011). Here, brown trout diet was mainly composed of aquatic and terrestrial predators that are likely to be the most valuable prey (larger with high energetic value and/or lower capture time) compared with other prey groups. However, this idea is not fully supported by our data as only the consumption of aquatic predators, not terrestrial predators, had a significant positive effect on individual growth rate, a proxy of fitness. It would be of great interest to examine the long-term repeatability on individual specialization and its ultimate consequences on individual life-history traits such as reproduction and survival.

In conclusion, we found that individual variability in trophic ecology, driven by human-induced modifications of environmental conditions that affect food resource availability and ecological opportunities, induces complex consequences at both individual and population levels. As the specialization on aquatic predators by brown trout was found to increase individual performances, we speculate that individual trophic specialization could, in turn, affect many ecological properties. Harmon *et al.* (2009) revealed that individual variability in resource use could affect ecosystem functioning. However, the potential effects of individual trophic specialization at higher levels of biological organization remain poorly explored, and we argue that further studies should investigate the relative importance of individual trophic specialization on ecosystem functioning.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Habitat characteristics and effect of specialization on individual growth rate.

Table S1. Physical and environmental characteristics of the 10 studied stream sites.

Fig. S1. Age-dependent effect of the dietary contribution of aquatic predators (%) on growth rate of recaptured individuals (% month^{-1}).

Appendix S2. Stable isotope analyses

Fig. S2. δ^{13}C and δ^{15}N values of individual fish (diamonds) and putative prey (circles) analysed in April (*left panels*) and September (*right panels*) in the 10 studied stream sites: MOUS (a, b), FRAI (c, d), PESQ (e, f), LAMP (g, h), PEYR (i, j), ORBI (k, l), BRG1 (m, n), LINO (o, p), BRG2 (q, r) and BERN (s, t).