Oikos 126: 1439–1450, 2017
doi: 10.1111/oik.03787

Subject Editor: Monika Winder. Editor-in-Chief: Dries Bonte. Accepted 20 March 2017

Resource composition mediates the effects of intraspecific variability in nutrient recycling on ecosystem processes

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Despite the growing evidence for individual variation in trophic niche within populations, its potential indirect effects on ecosystem processes remains poorly understood. In particular, few studies have investigated how intraspecific trophic variability can modulate the effects of consumers on ecosystems through potential changes in nutrient excretion rates. Here, we first quantified the level of intraspecific trophic variability in 11 wild populations of the omnivorous fish *Lepomis gibbosus*. Outputs from stomach content and stable isotope analyses revealed that the degree of trophic specialization and trophic positions were highly variable between and within these wild populations. There was intrapopulation variation in trophic position of more than one trophic level, suggesting that individuals consumed a range of plant and animal resources. We then experimentally manipulated intraspecific trophic variability to assess how it can modulate consumer-mediated nutrient effects on relevant processes of ecosystem functioning. Specifically, three food sources varying in nutrient quality (e.g. plant material, macro-invertebrate and fish meat) were used individually or in combination to simulate seven diet treatments. Results indicated that intraspecific variability in growth and nitrogen excretion rates were more related to the composition of the diet rather than the degree of specialization, and increased with the trophic position of the diet consumed. We subsequently used microcosms and showed that critical ecosystem functions, such as primary production and community respiration, were affected by the variability in excretory products, and this effect was biomass-dependent. These results highlight the importance of considering variation within species to better assess the effects of individuals on ecosystems and, more specifically, the effects of consumer-mediated nutrient recycling because the body size and the trophic ecology of individuals are affected by a large spectrum of natural and human-induced environmental changes.

Within populations, trophic niches vary among individuals (Bolnick et al. 2003), which can have strong consequences on population dynamics and community structure (Araújo et al. 2011). Intraspecific trophic variability may also alter the extent to which and how species influence ecosystem functioning (Harmon et al. 2009), but the mechanisms underpinning these changes remain relatively unknown. Consumers can exert top–down control through resource consumption, potentially causing cascading effects to lower trophic levels via density-mediated interactions (Pace et al. 1999). Simultaneously, they selectively sequester consumed nutrients into their body to meet their requirements for growth and reproduction (Sterner and Elser 2002). Excess nutrients and metabolic by-products are released via excretion and egestion, potentially enhancing the 'bottom–up' control of ecosystem processes (Glaholt and Vanni 2005, Knoll et al. 2009). Consequently, consumer-mediated nutrient recycling is an essential process within ecosystem dynamics, and predicting patterns of variation of excretion rates is relevant to better understanding the effects of consumers on ecosystem functioning (Taylor et al. 2015).

Early studies on consumer-mediated nutrient recycling have uncovered substantial interspecific variations in rates of nitrogen and phosphorus excretion, ultimately depending on elemental imbalance between consumers and their resources (Vanni et al. 2002, McIntyre et al. 2007, Small et al. 2011). High variations in excretion rates among conspecific individuals have also been reported (Villéger et al. 2012, El-Sabaawi et al. 2015a), with this potentially affecting ecosystem processes (Bassar et al. 2010, Taylor et al. 2012, El-Sabaawi et al. 2015b). Intraspecific variability in excretion rates is difficult to predict, as it might result from differences in both metabolic rate and trophic niche among individuals (Vrede et al. 2011). Intraspecific trophic variability may create variations in nutrient excretion rates of consumers by acting on the degree of specialization and the quality of the resource consumed, with the two factors potentially interacting. However, the relative importance of these two parameters is poorly understood, notably because

trophic specialization and diet composition are difficult to assess in wild populations (Bolnick et al. 2003). By foraging on a single prey, specialist individuals should display strongest nutrient imbalance with their resources compared to generalists, particularly if the mismatch is large (Frost et al. 2005). Therefore, individuals specialized on nutrient-rich resources are expected to release nutrient at higher rate than individuals foraging on nutrient-poor resources (Sterner and Elser 2002). In addition, specialist individuals are also predicted to have superior fitness than generalists (Bolnick et al. 2003). Alternatively, generalists might maximize their fitness by foraging on a resource assemblage made of nutritionally complementary resources (DeMott 1998). Diet mixing, by altering resource–consumer elemental imbalance, may lead to antagonistic or synergistic effects on nutrient excretion rates in generalist individuals.

Fishes are important regulators of biogeochemical cycles in freshwater ecosystems, due to their excretion of potentially limiting nutrients which are essential to support primary producers and heterotrophic microbes (Small et al. 2011, Capps and Flecker 2013). Fish diet composition varies considerably across trophic levels, ranging from herbivores consuming plant, phytoplankton and algal detritus to apex-predators consuming vertebrates, and including omnivores that feed across multiple trophic levels. These trophic groups often display striking differences in nutrient excretion rates, which are apparent at both the inter- and intraspecific levels (Villéger et al. 2012). Fishes are relevant examples of animals whose populations show considerable intraspecific trophic variability (Smith and Skúlason 1996, Bolnick et al. 2003), with individuals within populations often exhibiting a diversity of dietary strategies, from generalist to specialist (Quevedo et al. 2009, Svanbäck et al. 2015). For instance, the ratio of nitrogen and phosphorus excreted by Grizzard shad *Dorosoma cepedianum* was found to vary over nearly one order of magnitude among individuals, with dietary shifts suggested as mainly being responsible for this intraspecific variability in nutrient excretion rates (Pilati and Vanni 2007). This highlights the requirement to account for intraspecific trophic variability to better understand how fish can mediate nutrient recycling and, ultimately, affect the functioning of aquatic ecosystems.

The aim of our study was to quantify the effects of intraspecific trophic variability on consumer-mediated nutrient recycling and determine its potential consequences on relevant ecosystem processes. We selected the omnivorous fish *Lepomis gibbosus* as model species since it is an opportunistic omnivore that varies in its intensity of feeding on animals (e.g. macro-invertebrates and fish) and plant material (e.g. algae, macrophytes, wind-spread terrestrial seeds and detritus) (García-Berthou and Moreno-Amich 2000, Rezsu and Specziar 2006). It also displays a high level of intraspecific trophic variability (McCairns and Fox 2004, Bhagat et al. 2011). Using field and experimental approaches, the study was conducted in three phases: a field survey to quantify trophic specialization and diet composition in wild populations, a feeding experiment designed to test how specialization and diet composition influenced nutrient excretion rates and growth rates of fish, and a laboratory microcosm experiment used to assess effects of intraspecific variability of nutrient excretion rates on ecosystem processes. Stomach content and stable isotope analyses (SCA and SIA, respectively) were used in conjunction and performed on individuals of *L. gibbosus* originating from 11 lakes to determine extent of population heterogeneity as revealed by trophic specialization and difference in trophic position. In the laboratory, individuals of *L. gibbosus* were provided with diet differing in the number and type of food items to test for differences in nutrient excretion rates between specialists and generalists (Frost et al. 2005). We hypothesized that, independently of the diet quality, high level of specialization would lead to higher range of nutrient excretion rates within a population, given that diet diversity enables generalist individuals to cope better with nutrient imbalances than specialists (Frost et al. 2005). We also predicted that individuals feeding on nutrient-rich resource would excrete more nutrients (Sterner and Elser 2002, McIntyre and Flecker 2010). Finally, microbial microcosms supplied with excretion products released by fish during the feeding experiment were used to assess how intraspecific variation in nutrient excretion rates affected whole-system metabolism and litter decomposition. Increased nutrient availability through consumer recycling should stimulate rates of both autotrophic (primary production) and heterotrophic (respiration and litter decomposition) processes. Moreover, as decomposers are better competitors for nutrient resources than producers (Currie and Kalff 1984), it is also possible that heterotrophic processes respond more to fish excretion products addition than autotrophic processes.

Material and methods

Field survey of intraspecific trophic variability

To assess inter-individual variability in the trophic niches of *Lepomis gibbosus*, populations were sampled from 11 lakes that were former gravel pits in the flood plain of the Garonne River, France (Zhao et al. 2016). Sampling was completed in similar weather conditions (21 to 24°C, mixed cloud cover) between mid-September and mid-October 2012 by electrofishing along the littoral shoreline (Evangelista et al. 2015). To reduce biases between lakes in SCA related to the feeding period of consumers, one lake was sampled per day and electrofishing was conducted during the same period of time in each lake (between 1:00 to 3:30 p.m.). Captured individuals were immediately euthanized using an overdose of anaesthetic, stored on ice and frozen in the laboratory (–20°C) until subsequent processing. After defrosting, a subsample of 28 adult individuals (mean fork length = 79.0 mm ± 1.4 SE) was selected in each population when available (mean = 27.6 ± 1.2 individuals per population; Table 1), measured for fork length (FL ± 1 mm) and weighted (W ± 0.1 g). Stomach contents were dissected under a microscope and prey items were counted and identified to the lowest taxonomic level (mostly family level) for SCA (Supplementary material Appendix 1). Importantly, although present in stomach contents, plant debris (i.e. wind-spread seeds, algae, terrestrial detritus) could not be counted and were thus excluded from SCA. Whilst stomach content data provide information on the taxonomy of prey items, it has important limitations arising from their

Table 1. Mean value (± 95% CI or ± SE) and range of trophic niche (SEA_b), trophic position (TP) and individual specialization (PS_i) in each studied wild population (n = 11). The significance of PS_i was calculated using a Monte Carlo procedure: ***$p < 0.001$; **$p < 0.01$.

	SEA_b		TP			PS_i		
Lake	Mean (± 95% CI)	n‡	Mean (± SE)	Range	n‡	Mean (± SE)	Range	n‡
A	0.27 (0.18 – 0.37)	28	3.10 (0.02)	2.82–3.43	28	0.36 (0.05)***	0.09–0.62	12
B	0.38 (0.24 – 0.52)	28	3.13 (0.04)	2.85–3.72	28	0.83 (0.03)**	0.27–0.97	26
C	0.32 (0.21 – 0.44)	28	3.41 (0.03)	3.13–3.64	28	0.77 (0.03)***	0.22–0.92	26
D	0.30 (0.20 – 0.42)	28	3.40 (0.04)	2.89–3.94	28	0.59 (0.04)***	0.08–0.82	25
E	0.27 (0.18 – 0.37)	28	3.56 (0.03)	3.19–3.86	28	0.73 (0.04)***	0.15–0.92	28
F	0.32 (0.21 – 0.44)	27	3.29 (0.04)	2.67–3.74	27	0.67 (0.04)**	0.07–0.85	26
G	0.40 (0.26 – 0.55)	28	3.65 (0.06)	2.74–4.56	28	0.75 (0.05)***	0.05–0.95	26
H	0.35 (0.23 – 0.48)	28	3.61 (0.06)	3.16–4.34	28	0.42 (0.03)***	0.05–0.72	23
I	0.48 (0.31 – 0.67)	28	3.21 (0.07)	2.37–3.64	28	0.40 (0.03)***	0.10–0.77	28
J	0.32 (0.20 – 0.45)	24	3.35 (0.04)	3.01–3.63	24	0.81 (0.04)***	0.08–0.94	22
K	0.25 (0.17 – 0.35)	28	3.36 (0.02)	3.13–3.52	28	0.50 (0.04)***	0.08–0.78	26

‡Differences between the numbers of individuals used for stomach content and for stable isotope analyses were caused by the presence of empty stomachs.

representation of the diet of an individual as a single snapshot (i.e. several hours only); it can also underestimate the consumption of highly digestible prey. Consequently, the use of a complementary, temporally integrative approach to measure of intraspecific trophic variability was required, with this provided by SIA (Bolnick et al. 2003, Layman et al. 2012). The SIA was performed on the same individuals to assess trophic variability over a longer time period than SCA (Layman et al. 2012). Specifically, dorsal muscle samples were collected for stable isotope analyses of carbon ($\delta^{13}C$ value) and nitrogen ($\delta^{15}N$ value) which provide information on the origin of the resource consumed (e.g. littoral versus pelagic) and the trophic position of the consumers, respectively (Post 2002). Concomitantly, the putative prey resources of the fish were sampled from the littoral and pelagic habitats of the lakes with a pond net and with a 100-µm mesh net and an Ekman dredge, respectively (Supplementary material Appendix 1). Prior to analyses, all stable isotope samples were oven dried (48 h at 60°C), ground in a fine powder and subsequently analyzed at the Cornell Isotope Laboratory (Ithaca, NY, USA). The analytical precision for all samples, calculated as the standard deviation of an internal mink standard, was 0.11 and 0.12‰ for $\delta^{13}C$ and $\delta^{15}N$ values respectively.

Experimental approaches

Collection and rearing of experimental fish

Based on the field results, *L. gibbosus* were then collected from a single lake (area = 20.8 ha, mean depth = 3.7 m) whose trophic outputs indicated an intermediate level of trophic specialization, with a relatively large spectrum of prey consumed. On 3 October 2013, 81 individuals (FL: 65 to 75 mm) were captured in the littoral habitat using a seine net (5-mm mesh size) and then acclimated to laboratory conditions in three tanks (200 l, photoperiod: 12/12 h; water temperature: 17 to 18.5°C) over six weeks. The individual fish were fed ad libitum with commercial red maggots (*Diptera*) until the beginning of the experiment to minimize background variability in body elemental composition among individuals. During the mid-acclimation period, *L. gibbosus* were anaesthetized with eugenol (0.1 ml l^{-1}), measured for initial fork length ($FL_i \pm 1$ mm), weighed ($W_i \pm 0.1$ g), individually tagged with passive integrated transponder (FDX PIT-tags), and released into the 200 l-tanks after recovery in well-aerated water. At the end of the acclimation period, 48 individuals of the similar length range and age class were selected (FL_i range: 79–98 mm, mean ± SE 89.0 ± 0.8; age 1 + and 2 + years; Evangelista et al. unpubl.) for use in the experiment. The use of fish of similar lengths and ages limited the potential effects of ontogeny on the experimental data. The fish were transferred individually to 48 tanks filled with 50-l of dechlorinated tap water. Each tank was equipped with a filtration system, a plastic plant and a shelter. The 48 experimental units were distributed among six vertical shelving units (six blocks of eight treatments).

Effects of intraspecific trophic variability on nutrient recycling rates

During the laboratory experiment (nine weeks), fish were provided with one of three diets that comprised of one, two, or three food items in order to simulate three levels of decreasing trophic specialization. Using the diet data from experiment, trophic specialization was calculated as the diet overlap between an individual i and all individuals used in the experiment (i.e. the population) using the proportional similarity index PS_i, calculated following Bolnick et al. (2002) (Supplementary material Appendix 2). PS_i varies from 0 (no overlap) to 1 (total overlap). Here, PS_i ranged from 0.33 for specialist individuals and 0.99 for generalist individuals, and the PS_i of intermediate individuals was 0.66 (Fig. 1). The items represented vegetable matter (cooked white rice [R]), macro-invertebrates (chironmonid larvae [C]) and fish (grounded rainbow trout dorsal muscle with skin [F]). These items were used as they represented the three different reported trophic levels of *L. gibbosus* prey (García-Berthou and Moreno-Amich 2000) and cover a broad range of elemental composition (Fig. 1). White rice was selected as a plant-based source because it is readily available in a standardized size and quality and could mimic the quality of plant seeds and angling bait that are consumed by *L. gibbosus*. Rice was cooked to obtain a texture similar to the texture of plant seeds and angling bait after they have spent several days in water. Where mixtures of two and three items were used as

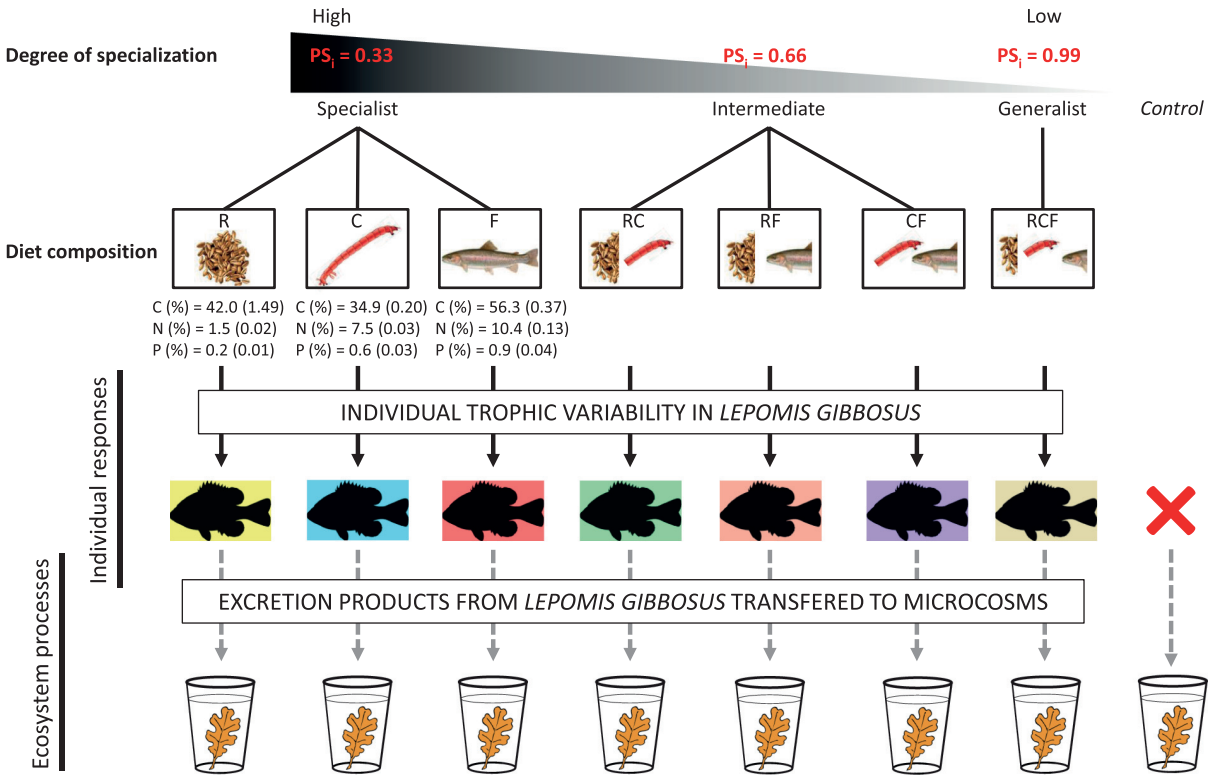

Figure 1. Schematic representation of the experimental design used to test the indirect effects (i.e. through nutrient recycling) of inter-individual trophic variability on individuals and ecosystem functioning. Trophic variability was manipulated with diet elemental composition nested under degree of specialization. Replicated treatments were dispatched in six vertical shelving units (blocks). The degree of individual trophic specialization (PS_i) was 0.33, 0.66 and 0.99 for specialist, intermediate and generalist treatments, respectively. Abbreviations: R: cooked rice; C: chironomid larvae; F: fish meat.

the diet, their total wet mass partitioned equally among the items. The diets were hand-fed to *L. gibbosus* using a daily ration of 3% of individual initial body mass (Glaholt and Vanni 2005). Mixed diets (i.e. intermediate and generalist) were homogenized manually to reduce potential bias towards the consumption of potential preferred item(s), while also maintaining item size.

The experimental design composed of seven treatments (Fig. 1): three types of specialists feeding on a single diet item (cooked rice [R], chironomid larvae [C] or fish meat [F]), three types of intermediates feeding on a mixture of two diet items (cooked rice × chironomid larvae [RC], cooked rice × fish meat [RF] or chironomid larvae × fish meat [CF]), and one generalist type feeding on an even mixture of all the diet items (cooked rice × chironomid larvae × fish meat [RCF]). There were six replicates for each specialist and intermediate treatment, and twelve replicates for the generalist treatment to fully account for higher variability in the mixture that arose from the homogenization of the dietary items. Individuals were randomly assigned to each treatment and there was no significant difference in the mean W_i and FL_i between treatments at the start of the experiment (ANOVA, $p = 0.178$ and $p = 0.07$ respectively).

Ammonium ($N\text{-}NH_4^+$, hereafter referred to as N) and soluble reactive phosphorus (SRP, hereafter referred to as P) excretion rates of *L. gibbosus* were quantified at the beginning of the experiment, just prior to the individuals being transferred in their experimental tanks (15 November 2013) and at the end of the experiment (16 January 2014). Per capita excretion rates (ER, hereafter referred to as 'excretion rate'; µmol ind.$^{-1}$ h^{-1}) were quantified, following Vanni et al. (2002). Two hours after feeding, *L. gibbosus* were incubated individually for 1.5 h in a plastic bag containing 0.8 l of spring water (Glaholt and Vanni 2005; see details in Supplementary material Appendix 2). Filtered water samples (80 ml filtered using Whatman GF/C, pore size 1.2 µm) were analyzed for N and SRP concentrations (Supplementary material Appendix 2) and excretion rates of N and P (µmol ind.$^{-1}$ h^{-1}) were calculated for each individual following Vanni et al. (2002):

$$ER_I = (([I]_{ind} - [I]_{control}) \times V)/t$$

where $[I]_{ind}$ and $[I]_{control}$ are the molar concentration (µmol l^{-1}) of the element I observed for fish and control, respectively, V is the volume (L) of spring bottled water in the plastic bag and t is the duration of the incubation (h) (Supplementary material Appendix 2). For each block, one control bag filled with bottled water but without fish was used to assess background levels of ammonium and phosphorus at the end of the excretion trials. Importantly, these excretion trials were performed every two weeks over the whole experimental period to renew the microcosm water but without quantifying nutrient concentrations. At the end of the experiment, after the final excretion trial, *L. gibbosus* were euthanized using an overdose of anesthetic and weighed ($W_f \pm 0.1$ g).

Specific growth rate (SGR; % week^{-1}) during the experiment was calculated as follows:

$$SGR = 100 \times (\ln W_f - \ln W_i)/t$$

where t is the duration of the experiment (nine weeks).

Effects of consumer-mediated nutrient recycling on ecosystem functioning

Laboratory microcosms were used to assess the indirect effects of intraspecific trophic variability on aquatic ecosystem processes through changes in fish-mediated nutrient recycling. Microcosms were used to mimic relevant processes occurring in the benthic littoral zone occupied by *L. gibbosus* in the wild, because the ability to measure these processes *in-situ* is inherently challenging. Microcosms (n = 54, 48 for each experimental individual and six for each control) consisted of one-liter cylindrical containers initially filled with 0.25 l of dechlorinated water and initiated with 0.5 l unfiltered lake water containing an inoculum of autotrophic and heterotrophic microorganisms. They were supplied with oak *Quercus robur* leaf litter collected at abscission and cut into leaf discs of 15 mm diameter using a cork borer. Each microcosm received a set of 10 leaf discs that were previously weighed to the nearest 0.1 mg (mean = 164.83 mg ± 0.41 SE). Microbial communities were allowed to develop from 7 November to 22 November 2013 before the microcosms were gently emptied until there was 0.1 l of water left in order to avoid losing particulate matter that remained on the bottom of the microcosm. Microcosms were then immediately supplied with 0.8 l of water containing fish excretory products (or clean spring water for controls) from fish excretion trials of 22 November 2013. During the experiment (54 days), microcosm water was renewed on four occasions with excretion products from trials spaced two weeks apart (i.e. 22 November, 5 and 19 December and 2 January 2014), and following the same procedure as described above. Microcosms were exposed to a 12 h light : 12 h dark photoperiod (mean instantaneous light intensity = 252.1 µmol m^{-2} s^{-1} ± 10.3 SE) at the laboratory temperature (17.0–18.5°C). They were assigned to the 48 experimental individuals and replicates were arranged in six blocks, corresponding to the level and the side (left or right) of a three-shelf unit.

Whole-microcosm metabolism, the standing biomass of algae and leaf-decaying fungi, litter mass loss rate and particulate nutrient concentration were assessed at the end of the experiment. The side of each microcosm was gently brushed to remove the biofilm, content was homogenized with blender and 0.06 l of water was filtered onto a Whatman GF/C filter. Filters were then oven-dried (60°C for 48 h) and used to quantify the amounts of particulate nutrients (N and P; µmol). Gross primary productivity (GPP) and community respiration (CR) were quantified using diurnal changes in oxygen levels (following Harmon et al. 2009). Using an optical DO probe, dissolved oxygen (DO) was measured (optical DO probe; Hach HQ10, LDO) right after the light was switched on (t_0, sunrise), and after 12 h (t_1, sunset) and 24 h (t_2, following sunrise) to capture daytime and night-time variations. Daily CR and GPP (mg O_2) was calculated as follows:

$$CR = (DO_{t1-t2}) \times 2 \times V \text{ and } GPP = (CR + DO_{t1-t0}) \times V$$

where V was the volume of water in microcosms (0.9 l). Total algal standing biomass (µg) was assessed based on the chlorophyll-a concentration and a subsample of 0.1 l of homogenized water was filtered onto a Whatman GF/F filter (pore size 0.45 µm) stored in the dark at –20°C until analysis. Chlorophyll-a was extracted in 90% acetone for 24 h and its concentration was determined with a spectrophotometer following Steinman et al. (2006). Before quantifying algal biomass, the leaf discs were gently removed from the microcosms, washed with deionized water, and freeze-dried to estimate the final litter mass. The remaining leaf material was coarsely crushed and an aliquot (mean = 21.60 mg ± 0.13 SE) was used to determine the ergosterol content in the leaf litter as a surrogate of fungal biomass (mg g^{-1} of litter). Ergosterol was determined using high-performance lipid chromatography and was converted into dry mass using a factor of 182 (Gessner and Chauvet 1993). The rate of litter decomposition (k in day^{-1}) was calculated as follows:

$$k = -\ln (M_f/M_i)/t$$

where M_f and M_i are the final and initial freeze-dried mass of leaf litter remaining in the microcosm, respectively, and t is the duration of the microcosm experiment (54 days).

Statistical analyses

Intraspecific trophic variability in wild populations

To ensure long-term comparisons of diet variability between and within populations, $\delta^{13}C$ and $\delta^{15}N$ values of each *L. gibbosus* were used to calculate a measure of trophic position (TP) and the corrected carbon isotope ratio ($\delta^{13}C_{cor}$) adjusted for between-population variation in stable isotope baselines following Post (2002) (Supplementary material Appendix 1):

$$TP = \lambda_{base} + (\delta^{15}N_{ind} - [\delta^{15}N_{lit} \times \delta^{13}C_{cor} + \delta^{15}N_{pel} \times (1 - \delta^{13}C_{cor})])/\Delta_N$$

$$\delta^{13}C_{cor} = (\delta^{13}C_{ind} - \delta^{13}C_{pel})/(\delta^{13}C_{lit} - \delta^{13}C_{pel})$$

where λ_{base} is the trophic position of the littoral and pelagic baseline ($\lambda_{base} = 2$), $\delta^{15}N_{ind}$ is the stable isotope value of the *L. gibbosus*, $\delta^{15}X_{lit}$ and $\delta^{15}X_{pel}$ are the stable isotope values of the littoral and pelagic baselines and Δ_N is the trophic enrichment factor obtained from previous studies ($\Delta_N = 3.4$; Post 2002). Using these baseline-corrected isotope values that allow comparison between populations, the size of the isotopic niche of each population was calculated using Bayesian standard ellipse area (SEA_b, 10 000 simulations) using stable isotope Bayesian ellipse in R (SIBER; Jackson et al. 2011) from the SIAR package (Parnell et al. 2010). This ellipse-based metric focuses on the core area of the isotopic niche and low values (i.e. low stable isotope area) indicate small isotopic niches. In addition, Kruskall–Wallis test was used to test for significant differences in trophic position between wild populations of *L. gibbosus*.

Based on SCA, PS_i was calculated (Supplementary material Appendix 1) and the overall degree of individual specialization (IS) in each population was then determined as the average PS_i of all individuals (Bolnick et al. 2002). For the sake of clarity, the index V = 1 – IS was used in the present study, with values closer to 1 indicating a high level of trophic specialization in the population. Significant

differences in the level of specialization between wild populations were tested using Kruskall–Wallis test. Generalized linear mixed-effects model (package lme4 ver. 1.1.10; Bates et al. 2015), with site as a random factor, tested the effect of body size on diet variation, with PS_i and FL used as independent and dependent variables respectively. Since PS_i varied between 0 and 1, the model specified a binomial family with a logistic link function.

Effects of intraspecific trophic variability on nutrient recycling rates

Two-way nested analysis of variance (ANOVA) tested the response of fish (growth and excretion rates) to the experimental treatments. In the experimental design, diet composition (defined as the number and types of food items: each item singly: [R]-[C]-[F], each item pair: [RC]-[RF]-[CF], and the three-items combination: [RCF]; Fig. 1) was nested in trophic specialization (the number of food items supplied to fish: 1-2-3; Fig. 1). The nested design was analyzed using the linear model:

$$Y_{ijk} = \mu + \alpha_i + \beta_{j(i)} + \varepsilon_{ijk}$$

where Y_{ijk} is the rate of growth or excretion of the k*th* fish fed with the j*th* type of diet within the i*th* level of specialization, α_i is the effect of i*th* level of specialization, $\beta_{j(i)}$ is the effect of the j*th* diet nested in the i*th* level of specialization, and μ and ε_{ijk} are the intercept and residual error of the model respectively. Two error terms are required for significance testing: specialization was tested against diet composition and diet composition against residual error (Quinn and Keough 2002). Tukey's post hoc test was used to determine which pairs of diet type significantly differed. Because excretion rates are a function of size, allometry was integrated into the analyses of nutrient excretion rates by dividing per capita excretion rates by W_f raised to the 3/4 power (mass-normalized per capita excretion rates; Torres and Vanni 2007). Non-additive effects of diet mixing on response variables were evaluated through a comparison of the observed versus expected values using one-sample paired t-test. Specifically, for each mixed-diet treatment (three intermediates and one generalist), the expected value was calculated as the mean value of specialist fish fed with either one of the food items. Given the multiplicity of comparisons involved, the false discovery rate (FDR; Benjamini and Hochberg 1995) procedure was applied to correct for alpha inflation using the *p.adjust* function (base-package ver. 3.1.2; <www.r-project.org>). The significant results after the FDR procedure are reported.

Effects of consumer-mediated nutrient recycling on ecosystem functioning

The general effects of the presence of excretory products on ecosystem processes were evaluated by comparing nutrient-less (i.e. control) with all treatments that contained fish excretory products using t-tests. Linear models were used to examine effects of amounts of excretory products (per capita N and P excretion rates) on ecosystem processes measured in the microcosms (i.e. particulate nutrient content, gross primary productivity, community respiration, algal standing biomass, fungal biomass on leaves and litter decomposition rates). To assess the mass dependence of nutrient excretion effects on ecosystem processes, linear models were also performed with mass-normalized per capita excretion rates and ecosystem processes as independent and dependent variables, respectively. Linear models were built with a block effect as covariate to control for potential variation in the experimental set-up. The assumption of homoscedasticity and the normality of the residuals for linear models and nested ANOVA were checked graphically using Tukey Ascombe and Q-Q plots, respectively. Prior to all statistical analyses, nutrient excretion rates and fungal biomass were $\log_{10}$ transformed and growth rate was square-root transformed. Highly influential data points were identified by the Cook's distance (D_i) plot and values were considered as critical for $D_i > 4/N$, where N is the number of observations (Bollen and Jackman 1990). Critical values were removed from the dataset prior the model was refitted. All statistical analyses were performed using R ver. 3.1.2.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.t24r0> (Evangelista et al. 2017).

Results

Intraspecific trophic variability in wild populations

Isotopic niche size (SEA_b, mean = 0.33 ± 0.02 SE) could increase up to two times between populations, ranging from 0.25 up to 0.48 (Table 1, Supplementary material Appendix 1 Fig. A1), indicating that variations in isotopic niche across populations were apparent when the temporally integrated SIA was used. In addition, trophic position significantly differed between populations (Kruskal–Wallis, $H = 127.31$, $p < 0.001$). Within-populations, SIA also indicated relatively high variability in trophic position, with the range of trophic position extending over more than one trophic level in several cases (mean TP = 3.37 ± 0.06 SE, mean within-population range = 1.32 ± 0.05 SE; Table 1, Supplementary material Appendix 1 Fig. A1). These results suggested that individuals of *Lepomis gibbosus* integrate across a wide range of resources with different trophic positions (i.e. from primary producer to secondary consumer), as individuals feeding exclusively on invertebrates would have a trophic position of 3.

SCA revealed that the level of trophic specialization (V ranging from 0.17 to 0.64; mean = 0.38 ± 0.05 SE) was significantly different between populations (Kruskal–Wallis, $H = 144.62$, $p < 0.001$). Within populations, individual specialization (PS_i) was highly variable (Table 1, Supplementary material Appendix 1 Fig. A2) and increased nine-fold on average among individuals (Table 1). The relationship between FL and PS_i was not significant (GLMM, $z = 0.55$, $p = 0.581$).

Effects of intraspecific trophic variability on nutrient recycling rates

Laboratory experiment revealed that individual growth rate did not vary significantly with the degree of specialization

Table 2. Results of the nested ANOVAs used to assess the effects of diet composition nested under degree of specialization on growth (% week^{-1}; square-root transformed) and the mass-normalized N and P per capita excretion rates (µmol g$^{-3/4}$ h^{-1}; $\log_{10}$ transformed) of *Lepomis gibbosus*. Significant p-values are in bold.

Response variables	Source	df	Mean squares	F	p	Eta-squared
Growth rate	degree of specialization	2	0.476	0.34	0.627	0.13
	diet composition	4	1.415	87.72	**<0.001**	0.78
	error	38	0.016			
N excretion rate	degree of specialization	2	0.011	0.07	0.897	0.03
	diet composition	4	0.156	36.01	**<0.001**	0.76
	error	41	0.004			
P excretion rate	degree of specialization	2	0.064	1.66	0.164	0.14
	diet composition	4	0.039	2.34	0.072	0.17
	error	39	0.016			

but was significantly affected by diet composition (nested ANOVAs, $p = 0.627$ and $p < 0.001$, respectively; Table 2). Specialists feeding on fish meat exhibited higher growth rates than individuals feeding on rice (Fig. 2A) and values obtained from mixed diet were not significantly different from predicted values based on mixing of single values ($p > 0.227$).

At the end of the experiment, the excretion rates of individual *L. gibbosus* displayed a wide range of variation among individuals, ranging from 4.12 to 22.61 µmol N ind.$^{-1}$ h^{-1} and from 0.04 to 0.29 µmol P ind.$^{-1}$ h^{-1}, but mass-normalized excretion rates did not significantly differ between degrees of diet specialization (nested ANOVAs, $p = 0.897$ and $p = 0.164$, respectively; Table 2). Diet composition significantly affected mass-normalized N excretion rate (nested ANOVA, $p < 0.001$; Table 2, Fig. 2B) whereas it did not significantly affect mass-normalized P excretion rate (nested ANOVA, $p = 0.072$; Table 2, Fig. 2C). Mass-normalized N excretion rate was significantly different for the three specialist treatments, with the highest and lowest excretion rates for fish specialized on fish meat (mean = 19.11 µmol N ind.$^{-1}$ h^{-1} ± 1.11 SE) and rice (mean = 5.94 µmol N ind.$^{-1}$ h^{-1} ± 0.47 SE), respectively (Fig. 2B). In general, these results suggested that the presence of fish meat within a diet also containing rice (i.e. [RF] and [RCF]) increased mass-normalized N excretion rate when compared to specialists feeding on rice (Fig. 2B). In parallel, intermediate individuals feeding on rice and chironomids excreted N nutrients at similar rates to specialists feeding on rice (Fig. 2B). For both N and P mass-normalized excretion rates, additive effects were observed for all mixed-diet treatment ($p > 0.059$).

Effects of consumer-mediated nutrient recycling on ecosystem functioning

Particulate N and P contents, gross primary production (GPP), community respiration (CR), and algal standing biomass (chlorophyll-a) were higher in microcosms supplied with fish excretory products than in control microcosms (t-tests, $p < 0.05$). Linear models showed that particulate N content, GPP and CR increased significantly with N excretion rate and that particulate P content and algal standing biomass increased significantly with P excretion rate (Table 3, Fig. 3). In contrast, whole-system metabolism did not change with P excretion rate (linear models, GPP: $F = 2.25$, $p = 0.142$ and CR: $F = 1.83$, $p = 0.184$; Table 3, Fig. 3B, 3D) and differences in algal standing biomass among microcosms were inconsistent with intraspecific variation in N excretion rate (linear model, $F = 0.12$, $p = 0.732$; Table 3, Fig. 3E). No difference was detected for the biomass

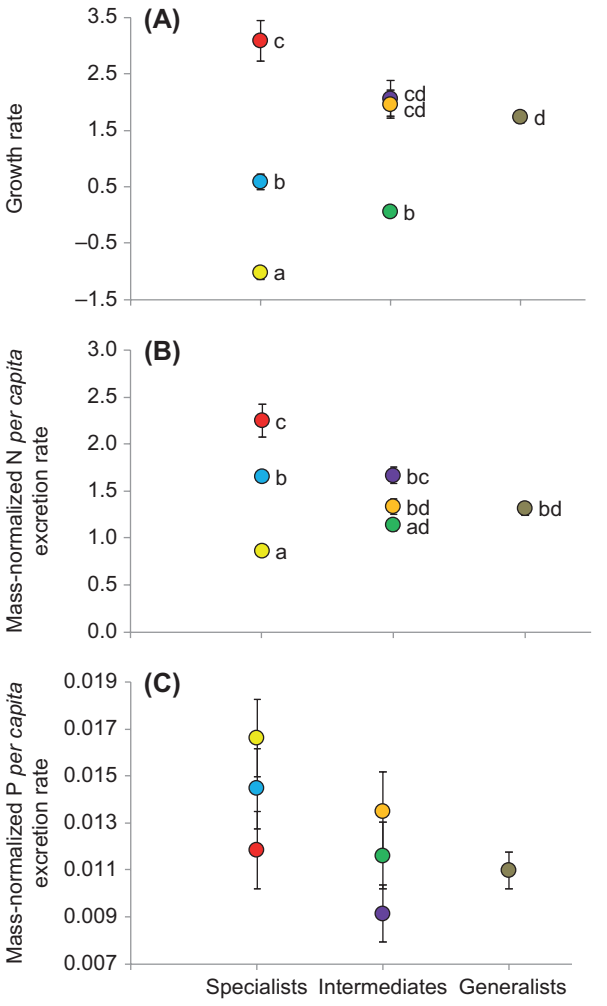

Figure 2. Effects of diet elemental composition treatment nested under degree of specialization treatment on mean (± SE) (A) growth rate (% month^{-1}) and (B) N and (C) P mass-normalized per capita excretion rates (µmol g$^{-3/4}$ h^{-1}). Colored dots represent rice specialists (yellow), chironomids specialists (blue), fish specialists (red), intermediates rice × chironomids (green), intermediates rice × fish (orange), intermediates chironomid × fish (purple) and generalists (dark green). Different letters indicate significant differences among these means (Tukey's HSD, $p < 0.05$).

Table 3. Results of the linear models assessing the relationships between N and P per capita (μmol ind.$^{-1}$ h^{-1}; $\log_{10}$ transformed) and mass-normalized per capita excretion rates (μmol g$^{-3/4}$ h^{-1}; $\log_{10}$ transformed) and ecosystem processes: nutrient particulate content (μmol), gross primary productivity (mg O_2), community respiration (mg O_2), algal standing biomass (μg), fungal biomass (mg; $\log_{10}$ transformed) and litter decomposition rate (day^{-1}). Significant p-values are in bold.

			Per capita excretion rates			Mass-normalized per capita excretion rates		
Response variables	Source	df	Mean squares	F	p	Mean squares	F	p
Particulate N concentration	block	5	24 490	4.84	**0.002**	24 491	4.43	**0.003**
	N excretion rate	1	34 660	6.85	**0.013**	19 123	3.46	0.071
	P excretion rate	1	2070	0.41	0.526	219	0.04	0.843
	residuals	37	5058			5528		
Particulate P concentration	block	5	12.58	33.5	**<0.001**	12.61	29.16	**<0.001**
	N excretion rate	1	0.93	2.48	0.124	0.003	0.01	0.934
	P excretion rate	1	2.67	7.11	**0.011**	1.06	2.45	0.126
	residuals	37	0.38			0.43		
Gross primary productivity	block	5	6.63	2.34	0.061	6.32	2.16	0.080
	N excretion rate	1	15.07	5.32	**0.027**	3.22	1.10	0.302
	P excretion rate	1	6.39	2.25	0.142	5.20	1.77	0.191
	residuals	37	2.84			108.51		
Community respiration	block	5	4.20	2.36	0.058	4.05	2.10	0.087
	N excretion rate	1	8.20	4.62	**0.038**	4.64	2.41	0.129
	P excretion rate	1	3.26	1.83	0.184	1.76	0.91	0.345
	residuals	38	1.77			1.93		
Algal standing biomass	block	5	2115	0.27	0.927	3695	0.46	0.805
	N excretion rate	1	935	0.12	0.732	12327	1.53	0.224
	P excretion rate	1	88245	11.21	**0.002**	49079	6.08	**0.018**
	residuals	38	7871			8072		
Fungal biomass	block	5	0.17	3.72	**0.008**	0.17	3.72	**0.008**
	N excretion rate	1	0.01	0.19	0.664	0.02	0.39	0.538
	P excretion rate	1	0.02	0.46	0.500	0.01	0.26	0.610
	residuals	37	0.05			0.05		
Litter decomposition rate	block	5	1.33×10^{-06}	0.42	0.829	1.33×10^{-06}	0.42	0.829
	N excretion rate	1	2.91×10^{-07}	0.09	0.763	2.12×10^{-06}	0.67	0.417
	P excretion rate	1	2.62×10^{-06}	0.83	0.367	6.94×10^{-07}	0.22	0.642
	residuals	37	3.15×10^{-06}			3.15×10^{-06}		

of leaf-associated fungi and litter decomposition rate between treatment and control microcosms (t-tests, $p = 0.656$ and $p = 0.672$, respectively; Fig. 3K–3L). Intraspecific variation in nutrient excretion rates did not explain differences in these ecosystem properties among microcosms that were supplied with fish excretory products (linear models, $p > 0.367$; Table 3, Fig. 3G–3J). Except for algal standing biomass (linear model, $F = 6.08$, $p = 0.018$; Table 3), effects of N and P excretion rates on ecosystem properties were not statistically significant with mass-normalized excretion rates (linear models, $p > 0.071$; Table 3), indicating that consumer-mediated effects on ecosystem processes were primarily driven by the effects of diet treatment on individual body mass through differences in growth rate.

Discussion

The widespread occurrence of diet variability within populations is now recognized, although its incidence and implications at the higher levels of biological organization remain poorly understood (Bolnick et al. 2003, Araújo et al. 2011). Here, we observed that intraspecific trophic variability occurred between and within wild populations of *Lepomis gibbosus*. This was partly due to high variability in both the degree of individual specialization and their trophic position quantified using SCA and SIA. Variability in trophic position also suggested that individuals consumed a range of plant and animal resources. The experimental approaches then indicated that the rate of nutrient excretion was influenced by diet composition but did not change with the degree of specialization. Specifically, N excretion rate increased with diet quality but P excretion rate did not change with diet composition. Finally, we found that increased nutrient excretion rates potentially enhanced integrative ecosystem processes through biomass-dependent effects.

Generalist populations with wide trophic niches are composed of more heterogeneous individuals using only a subset of the available prey (Bolnick et al. 2003). Here, we found that trophic specialization differed widely among coexisting individuals of *L. gibbosus* and such trophic variability was consistently detected within the eleven wild populations surveyed. In addition, omnivorous *L. gibbosus* individuals did not occupy the same trophic position, as evidenced by stable isotope analyses that reflect dietary information over several months (Layman et al. 2012). Clearly, individuals within populations differed in respect of the relative contribution of plant- versus animal-derived resources to diet, as supported by the wide range of observed trophic position values. Plant material was commonly found in the stomach content of *L. gibbosus* in the present and previous studies (García-Berthou and Moreno-Amich 2000, Rezsu and Specziar 2006) and may be ingested while fish foraged on benthic prey embedded within sediments or

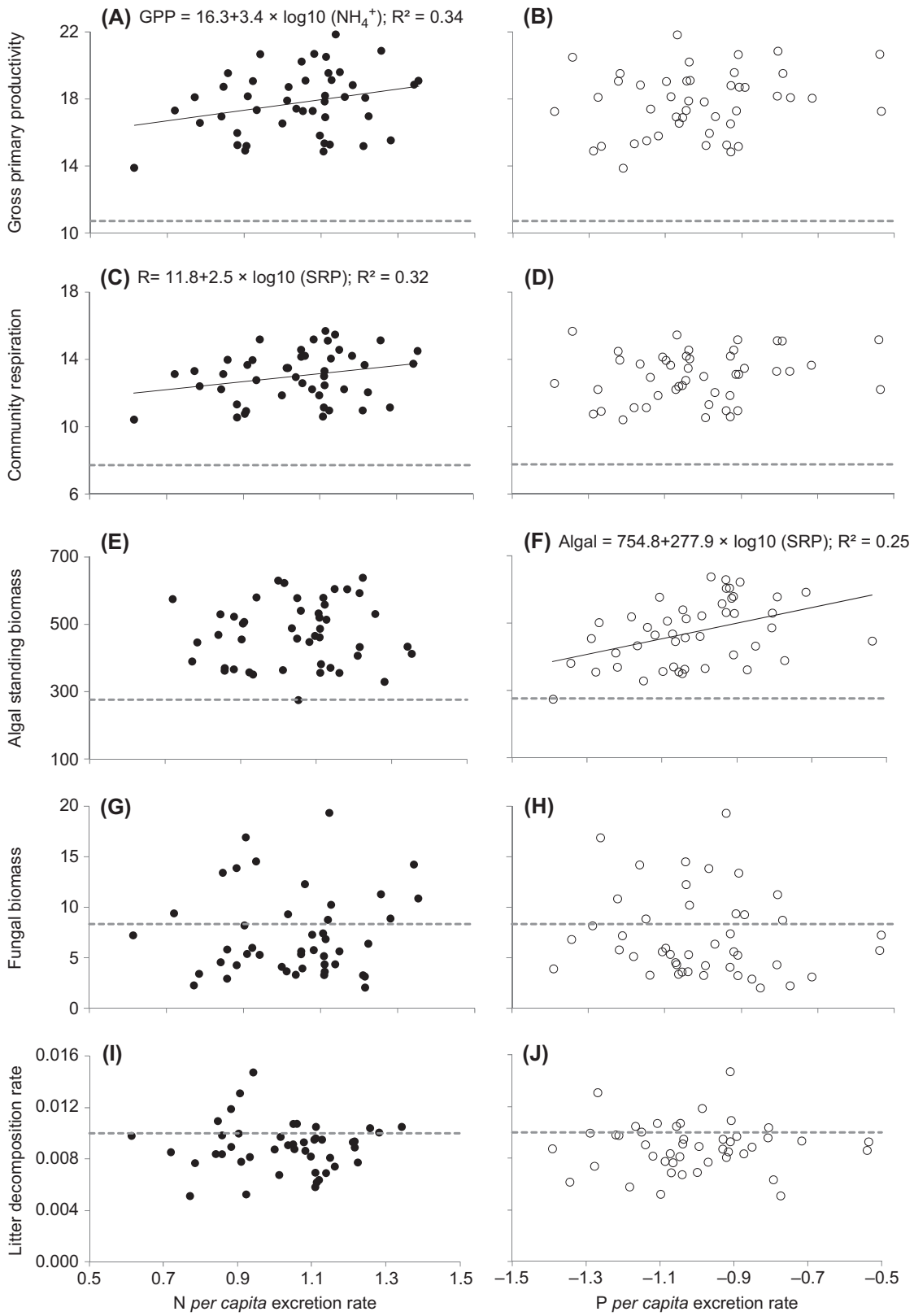

Figure 3. Relationship between N (left panels) and P (right panels) per capita excretion rates (µmol ind.$^{-1}$ h^{-1}; $\log_{10}$ transformed) and (A–B) gross primary productivity (mg O_2; n = 45), (C–D) community respiration (mg O_2; n = 46), (E–F) algal standing biomass (µg; n = 46), (G–H) fungal biomass (mg; n = 45) and (I–J) litter decomposition rate (day^{-1}; n = 45). Regression lines are displayed using continuous black lines with equations above each panel when significant. The dotted lines represent the mean value of the control microcosms.

macrophytes. While SCA suggested that *L. gibbosus* relied exclusively on invertebrate prey as animal food source, we cannot rule out that some individuals displaying a high trophic position also consumed fish-derived prey such as eggs and larvae (García-Berthou and Moreno-Amich 2000). For instance, in the present study, fish were sampled in late summer, i.e. at a time when fish eggs and larvae had become scarce since all co-occurring species have already spawned, which likely explained the absence of fish-derived prey in the stomach contents. Indeed, SCA provide only a snapshot of individuals' diets, unless repeated non-lethal stomach flushing are performed from the same individuals (Araújo et al. 2011). Nevertheless, SCA provided dietary information at the taxonomic level, with these data used to calculate trophic specialization based on count data. Since plant debris could not be quantified in the same way as animal prey, however, they were excluded from SCA and could not be including in the quantification of trophic specialization, which represents a limitation of this approach when using omnivorous model species. In contrast, SIA provides temporally-integrative information about individual diet, but precise quantification of the trophic niche can be difficult, particularly if putative resources are taxonomically distinct but isotopically similar. Therefore, the combined use of SIA and SCA is an appropriate way to counterbalance the limitations of each method to investigate the trophic ecology of omnivores. Variation in trophic enrichment factor can also be a source of uncertainty when quantifying the trophic position of wild organisms (Vander Zanden and Rasmussen 2001, Busst et al. 2015). Indeed, in omnivorous species, high variation in TEF has been reported between individuals consuming plant-based or animal-based diet (Busst and Britton 2016). However, in the present study, such potential variations in TEF among individuals were unlikely to affect our findings of the existence of strong variations in trophic position within and between wild populations.

The balanced diet hypothesis stipulates that generalist individuals consuming multiple prey have access to a more complete range of nutrients than specialist individuals, which could provide fitness benefits (DeMott 1998). Our laboratory experiment did not support this hypothesis, as diet mixing did not increase individual growth. By contrast, growth rates were higher for individuals feeding on the single best-quality food item, whereas specialization on poorer-quality diet might induce low or negative growth rate (Lefcheck et al. 2013). These findings thus indicate that diet specialization toward high quality food may confer fitness advantages in generalist populations. However, in natural situations, consumers specializing on high food quality may expend more energy to capture their prey. For instance, predation on fish eggs can induce fighting costs and reciprocal predation, particularly in nest-guarding species (Baldridge and Lodge 2013). In parallel, species providing parental care, such as *L. gibbosus*, can also display cannibalism, particularly when guarding is costly (Manica 2002). Thus, specializing on high quality food may induce contradictory effects in fish in natural environments, although this requires further investigations.

Nutrient cycling measured as per capita excretion rates was highly variable among individuals (ranging from to 4.12 to 22.61 μmol N ind.$^{-1}$ h^{-1} and from 0.04 to 0.29 μmol P ind.$^{-1}$ h^{-1}, respectively). These values were within the range reported by Villéger et al. (2012) for wild populations of freshwater fish species (ranging from 0.20 to 518 μmol N ind.$^{-1}$ h^{-1} and from 0.03 to 29.34 μmol P ind.$^{-1}$ h^{-1}). They were, however, slightly lower than the values observed for *L. gibbosus* (ranging from 13.46 to 26.12 μmol N ind.$^{-1}$ h^{-1} and from 0.13 to 1.74 μmol P ind.$^{-1}$ h^{-1}; Villéger et al. 2012). Although the effects of diet composition on consumer excretion rates can be difficult to predict (but see Moody et al. 2015), our findings revealed that individuals feeding at higher trophic position (i.e. those with an animal-based diet) excreted N at higher rates (Bassar et al. 2010). This is probably because animal items used in this study were nutrient-rich compared to rice and, correspondingly, consumers would release these nutrients at higher rates (Sterner and Elser 2002). Surprisingly, and contrary to findings reported in literature (Moody et al. 2015), we did not detect significant changes in P excretion rate in relation to intraspecific trophic variability. Fish require large amount of P that is allocated to the formation of bones and scales, and to somatic growth (Pilati and Vanni 2007, McIntyre and Flecker 2010). The diet items used in the present study were relatively low in P (from 0.2 to 0.9% dry mass; Fig. 1) and this could explain the high level of P retention by fish. For instance, the mean C:P ratios of diet items used in the experiment were higher (mean = 311.8 ± 221.8 SD) than the mean threshold elemental ratio of carbon and phosphorus (i.e. the nutrient ratio of an organism's diet where growth limitation of this organism switches from one element to another; Sterner and Elser 2002) of nine freshwater fish species reported in the literature (mean = 135.4 ± 44.4 SD; Frost et al. 2006). This indicates that fast growth *L. gibbosus* species (Copp and Fox 2007) was probably P-limited in our experiment, suggesting that consumers with an r- or k-strategy would potentially have different role in nutrient recycling.

Some of the integrative ecosystem processes measured during the present study differed substantially among microcosms (i.e. gross primary productivity and community respiration) and a significant fraction of this variability was driven by intraspecific variation in the rate of nitrogen excreted by fish. Because we also demonstrated that diet composition determined nitrogen excretion rate, it indicated that intraspecific trophic variability can alter ecosystem functioning through consumer-mediated nutrient recycling (Bassar et al. 2010, Taylor et al. 2015). Based on our findings, specialization toward resources with higher trophic level should exacerbate the effects of individual fish excretion on ecosystem functioning. Previous studies have demonstrated that increased nutrient quantity through loading can shape consumer-mediated nutrient recycling, probably through changes in population biomass and/ or community structure (Vanni et al. 2005, Wilson and Xenopoulos 2011). Here, we found that the biomass dependence of fish excretion can also occur within the same cohort and mediate the effects of consumers on ecosystem functioning. This highlights the importance of integrating body size variation in assessments of the effects of intraspecific variability on ecosystem functioning (Rudolf and Rasmussen 2013). In addition, since human activities can affect body size distribution in wild population (Evangelista et al. 2015), it would be of interest to assess how they affect the relative importance

of consumer-driven nutrient recycling along a gradient of perturbation, such as anthropogenic eutrophication.

The amount of N and P associated with fine particulate organic matter increased with the inputs of fish excretory products, but also as a result of microbial immobilization of dissolved inorganic nutrients. Primary producers and decomposers rely on inorganic nutrients for growth and metabolism (Daufresne and Loreau 2001). In our experiment, neither decomposition rate of coarse particulate organic matter nor fungal biomass were modified by the addition of excretory products, suggesting that litter-associated decomposers did not use fish-derived nutrients. Therefore, and contrary to our prediction, producers may have contributed substantially to nutrient immobilization in microcosms as evidenced by the positive response of GPP and algal biomass to fish excretory products. Finally, the asymmetric responses between autotroph and heterotroph organisms observed here highlighted the complexity of ecosystem processes responses to nutrient loading. Although these results are not trivial, we argue that future investigations are needed in less contrived experimental environments. This would help to fully encompass other additional effects that might modulate and interact with the relationship between nutrient recycling and ecosystem processes (Knoll et al. 2009, Bassar et al. 2010, Taylor et al. 2012).

A large number of studies have demonstrated that changes in community structure or population size can influence consumer-mediated nutrient recycling (Vanni et al. 2002, McIntyre et al. 2007, Pilati and Vanni 2007, Villéger et al. 2012, Allgeier et al. 2016). In the present study, we demonstrated that changes within populations can also induce variation in consumer nutrient excretion rates and ecosystem processes, providing a deeper understanding of the indirect role of consumers in regulating ecosystem functioning. Together, these findings highlight that the ecological effects induced by intraspecific variability in consumers may be strong compared to those induced by interspecific variability (Palkovacs et al. 2015). This would be particularly relevant in the current context of global changes in general and biological invasions in particular, as they can alter the diversity patterns of consumers both at the intraspecific and interspecific levels, affecting native organisms and recipient ecosystems across levels of biological organization (Buoro et al. 2016). We also argue that future studies would benefit to quantify the relative effects of top–down (direct and consumptive) and bottom–up (indirect and nutrient-mediated) mechanisms in controlling the effects of intraspecific variability on ecosystem functioning (Knoll et al. 2009, Taylor et al. 2015).

Acknowledgements – We are very grateful to the graviere team for their help during fish sampling and to N. Charpin and T. Zhao for their help during experiment. D. Lambrigot and F. Julien are thanked for their laboratory assistance. We also thank S. Villéger for constructive comments on earlier version of the manuscript. Authorizations to perform this study were provided by the "Arrêtés Préfectoraux - 31/07/2012 and 10/07/2013".

Funding – This work was supported by the ONEMA (Projet ISOLAC –Convention 13-V5-28), a Fisheries Society of the British Isles Research Grant, a PRES-Toulouse grant (Inva_Eco_Evo_Lac) and an "ERG Marie Curie" grant (PERG08-GA-2010-276969). CE and JC are part of EDB, part of the French Laboratory of Excellence project "TULIP" (ANR-10-LABX.41; ANR-11-IDEX-0002-02).

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Supplementary material (available online as Appendix oik-03787 at <www.oikosjournal.org/appendix/oik-03787>). Appendix 1–2.