

Effects of species vs. functional diversity: Understanding the roles of complementarity and competition on ecosystem function in a tropical stream fish assemblage



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ABSTRACT

The positive effects of biodiversity on the functioning of ecosystems are well demonstrated in laboratory microcosms but the precise mechanisms underlying higher ecosystem process rates in natural assemblages are less well understood. We investigated, under semi-natural conditions (field enclosures), the potentially interactive effects of species identity and trophic function (i.e., feeding guild) on consumer growth, using a fish assemblage in a tropical stream. We tested the relative importance of species identity and trophic function on consumer growth by placing 2 fish of either (i) the same species, (ii) different species but of similar trophic function, or (iii) different species of different trophic functions in each of 72 stream enclosures for 48 days and measuring biomass change, individual diet composition and behavior. We predicted that if functional diversity had a larger impact than species diversity, then fish growth would be highest for pairs of species from different functional groups (i.e., those with the highest diet complementarity), intermediate for different species within a guild, and lowest for the same species (those with the lowest complementarity and highest niche overlap), such that functional variation between species in different guilds would exceed functional differences within guilds. Our results show that functional heterogeneity rather than species diversity *per se* had the greatest impact on food resources used complementarily, leading to higher biomass accrual. Mechanistically, higher growth rates were driven by concomitant increases in resource intake and reductions in antagonistic interactions. Together, these results underscore the importance of functional diversity on macroconsumer production in natural assemblages.

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1. Introduction

Theory and ecological models suggest that species richness in ecological communities is promoted by relatively high levels of intra-specific competition paired with relatively low levels of inter-specific competition (low niche overlap; Hutchinson, 1959; MacArthur and Levins, 1967; Finke and Snyder, 2008). By definition, different species must be functionally dissimilar along axes of a Hutchinsonian space (*sensu* Rosenfeld, 2002), such that under conditions of minimal niche overlap, the exploitation of

available resources should be enhanced following the introduction of additional species in an assemblage (Tilman et al., 1997a; Loreau et al., 2001; Cardinale et al., 2002). Ample empirical evidence exists suggesting coupling between species richness and EF (Tilman et al., 1997a; Hooper et al., 2005; Cardinale et al., 2007). Consequently, high species richness at the community level should be coupled with elevated ecosystem process rates, often termed ecosystem functioning (EF), broadly defined in terms of energy transfer and matter cycling (Lawton, 1994; Chapin et al., 1997; Ghilarov, 2000; Hooper et al., 2005).

Higher EF is often argued to occur as a result of complementarity (minimal overlap) in resource use among functionally diverse species (Petchey and Gaston, 2002; Petchey, 2003; Hooper et al., 2005; Burkepile and Hay, 2008). Broadening of resource use under higher species diversity may increase EF by allowing more thorough exploitation/use of all available resources (Petchey, 2003; Heemsbergen et al., 2004). Thus, it may not be species *per se*

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but rather functional diversity in an assemblage that maximizes resource exploitation and ultimately EF (Hooper et al., 2005; Mokany et al., 2008).

Seminal experiments relating species richness to EF articulated the hypothesis that reduction in biodiversity can affect important ecological processes (reviewed in: Loreau et al., 2001; Cardinale et al., 2007; Fargione et al., 2007). These experiments focused on plant species richness and demonstrated that reducing the number of species led to less efficient use of soil nutrients and lower production of plant biomass, while species-rich assemblages showed highest levels of EF from resources used complementarily (Tilman et al., 1996, 1997b). Despite the demonstrated importance of complementarity in predicting how change in biodiversity may affect EF, a majority of studies explored the importance of species richness within narrowly defined sessile taxa (e.g., communities of plants, mycorrhizal fungi, macrophytes, bryophytes, sessile marine invertebrates), often under controlled laboratory/mesocosm conditions, while less emphasis has been placed on understanding the effects of diversity in organisms displaying more complex suite of behavior, or in complex natural habitats. Additionally, the importance of intra- vs. interspecific interactions for EF has been poorly considered (Worm and Duffy, 2003; Gamfeldt and Hillebrand, 2008). Frequently, only the net effect of all of the processes that resulted from complementarity among species is typically estimated (Lawton, 1994; Bunker et al., 2005), such that complementarity is more often inferred rather than directly demonstrated, leaving the mechanisms underlying changes in EF difficult to clearly identify (Chapin et al., 1997; Hooper et al., 2005; Mokany et al., 2008; but see Carey and Wahl, 2011). Understanding the specific mechanistic nature by which complementarity promotes EF requires assessing resource partitioning among competitors along relevant axes of a Hutchinsonian niche-space (e.g., food, space, or time; *sensu*, Wojdak and Mittelbach, 2007; Carey and Wahl, 2011). This requires realistic scenarios and experimental approaches if the mechanisms underlying diversity effects on ecosystem functioning are to be understood in real ecosystems.

Here, we sought to distinguish between the roles of taxonomic vs. functional identity on fluxes of energy into the production of fish biomass in a first-order tropical stream. Given that fish are the most speciose taxonomic group of vertebrates and exhibit a wide range of feeding modes related to their morphology and behavior (Pitcher, 1993; Nelson, 1994; Matthews, 1998), they are excellent candidates for manipulating taxonomic and functional trophic diversity. In addition, fish biomass production is a major pathway of energy flow at the population (Waters, 1977) and assemblage levels (Ivlev, 1966). Thus, by selectively manipulating both species identity and trophic functions (i.e., trophic guilds), their relative effect on EF (i.e., fish growth) and mechanisms of impact may be understood. For example, if species within a guild display highly similar interspecific functional attributes (i.e., if species are functionally equivalent or redundant), then adding additional species may not have any significant impacts on EF. In this case, functional diversity (i.e., increasing the number of trophic guilds)

should be the best predictor of increased function. In contrast, if species identity *per se* is important enough to broaden resource use and reduce competitive interactions, then species identity may be a good predictor of increased function – the core issue being relative variation in functional attributes within vs. between trophic guilds.

To test these alternative hypotheses, we measured EF in terms of growth in biomass for fish placed in enclosures in a tropical stream while simultaneously measuring dietary overlap between individuals, biomass of food intake, individual foraging rates and antagonistic behavior. We expected that increasing functional diversity would facilitate EF by broadening the overall diet breadth within an experimental fish assemblage and reduce dietary overlap otherwise incurred when fish of a single functional group occur together. Higher functional diversity should likewise promote an overall increase in the biomass of food items consumed by the fish assemblage, while reducing competitive interactions and increasing feeding behavior.

2. Materials and methods

2.1. Study

We conducted this experiment from January to April 2009 in Água Azeda Creek (approximately, 12°28'8.63"S, 37°57'4.41"W), a clear-water first-order tributary of the Imbassá River located in Mata de São João (Bahia, Brazil). This creek is located in a dense Atlantic rain forest with minimal direct anthropogenic impacts. The experiment was carried out in a section of the stream approximately 500 m long with high (70% or more) tree canopy coverage. The stream substratum consisted of sand with embedded leaf litter and small branches. The mean depth, bankfull channel width, water temperature, current velocity and turbidity were 0.19 m (ranging from 0.15 to 0.31 m), 2.38 m (ranging from 1.60 to 2.98 m), 24.1 °C (ranging from 24.0 to 24.4 °C), 4 cm s⁻¹ (ranging from 2 to 12 cm s⁻¹) and 7 NTU (ranging from 7 to 8 nephelometric turbidity units), respectively.

2.2. Fish species sampled

Sampling in the Água Azeda Creek allowed us to identify 10 fish species, 6 of which were used for the experiment (i.e., those found in sufficient numbers and exhibiting suitably contrasting functional characteristics; Table 1). These 6 fish species were *Astyanax altiparanae*, *Astyanax lacustris*, *Cichlasoma sanctifranciscense*, *Hoplerythrinus unitaeniatus*, *Hoplias malabaricus* and *Hoplosternum littorale*. Individuals of the selected species were caught using minnow traps, dip nets and a 4-mm seine net. To obtain a sufficient number of fish for the experiment, we also collected fish from two additional nearby unnamed streams and the Imbassá River into which all three streams drain.

We assigned the fish species used in this experiment to one of three trophic groups, based on the findings of previous studies: invertivore–omnivore, piscivore–invertivore or detritivore–

Table 1

Fish species used in the experiment. Focal species (indicated with asterisks) were used in all three treatments; companion species (°) varied with treatments.

| | Same species treatment | Similar trophic function treatment | Different trophic function treatment |
|-----------|------------------------------------|------------------------------------|--------------------------------------|
| Focal sp. | <i>C. sanctifranciscense</i> * I-O | <i>C. sanctifranciscense</i> * I-O | <i>C. sanctifranciscense</i> * I-O |
| Comp. sp. | <i>C. sanctifranciscense</i> ° I-O | <i>A. altiparanae</i> ° I-O | <i>H. littorale</i> ° D-B |
| Focal sp. | <i>A. lacustris</i> * I-O | <i>A. lacustris</i> * I-O | <i>A. lacustris</i> * I-O |
| Comp. sp. | <i>A. lacustris</i> ° I-O | <i>A. altiparanae</i> ° I-O | <i>H. littorale</i> ° D-B |
| Focal sp. | <i>H. malabaricus</i> * P-I | <i>H. malabaricus</i> * P-I | <i>H. malabaricus</i> * P-I |
| Comp. sp. | <i>H. malabaricus</i> ° P-I | <i>H. unitaeniatus</i> ° P-I | <i>H. littorale</i> ° D-B |

Functional trophic group: I-O = invertivore/omnivore; P-I = piscivore/invertivore, D-B = detritivore/benthivore.

benthivore. We used these feeding guilds to differentiate between similar and dissimilar trophic functional treatments. *A. lacustris* (Luz et al., 2009; Wolff et al., 2009), *A. altiparanae* (Garutti and Britski, 2000; Casatti, 2002) and *C. sanctifranciscense* (Wootton and Oemke, 1992) were classified as invertivore–omnivores; *H. malabaricus* (Luz-Agostinho et al., 2006; Teixeira de Mello et al., 2006) and *H. unitaeniatus* (Mérona and Rankin-de-Mérona, 2004) were classified as piscivore–invertivores; and *H. littorale* (Mérona and Rankin-de-Mérona, 2004; Luz-Agostinho et al., 2006) was classified as a detritivore–benthivore.

2.3. Experimental design

To assess the importance of taxonomic vs. functional identity (i.e., species vs. trophic diversity) on fish biomass gain, we devised three functional group treatments using three focal fish species (i.e., three target species that were used in all three functional group treatments) and three companion species (used in only a subset of treatments), such that nine experimental combinations were used (Table 1). Each treatment consisted of a pair of size-matched fish placed in an enclosure. The enclosures were circular in shape, with an area of $\sim 1.8 \text{ m}^2$, and were built using 7-mm plastic mesh embedded in the substratum to a depth of $\sim 30 \text{ cm}$ to prevent fish escape. The enclosures were placed in the central part of the creek and were separated from each other by a minimum of 5 m. In each enclosure, we placed two individuals of: (i) the same species (same species treatment); (ii) different species but sharing a common trophic guild (similar trophic function treatment) or (iii) different species with distinct trophic requirements (different trophic functions treatment). The trophic requirements included both the diet and the general feeding mode (e.g., benthic vs. drift/surface feeder). Table 1 shows the different treatments for the three focal species: *A. lacustris*, *C. sanctifranciscense* and *H. malabaricus*. These species were chosen on the basis of their functional attributes and the relative ease of finding sufficient numbers of individuals for testing.

We used 10 replicates per combination of treatments for each focal fish species. However, as we could not find enough individuals of *H. malabaricus*, we used four replicates per combination of treatments for this focal species. A total of 72 enclosures were stocked with pairs of fish (30 enclosures for *A. lacustris*, 30 for *C. sanctifranciscense* and 12 for *H. malabaricus*) and left for 48 days. Previous research showed that significant treatment effects may occur after only 35 days in fish assemblages (Carey and Wahl, 2011).

The order of treatments and the focal species used were randomly assigned to enclosures. At the end of the 48-day period, we recaptured and weighed all fish to the nearest 0.01 g (using a Ohaus Scout Pro Balance, Parsippany, NJ, USA), calculated the changes in fish weight from the start of the experiment (i.e., day 0) and collected the stomach contents of all of the fish. Fish biomass production was determined by relative growth [(final mass – initial mass)/initial mass] as in Carey and Wahl (2011). Only the biomass change of the focal fish species was used for analysis. However, in the ‘same species’ treatment, we averaged the biomass accrual of the two individuals. The stomach contents at the time of collection were fixed in 5% formaldehyde and preserved in 70% ethanol for later laboratory sorting and identification at $16\times$ magnification.

For every enclosure, we measured the depth (cm) at the centre, the proportion of the substratum covered by leaf litter and the local canopy cover (the estimated percentage of the sky blocked by foliage when viewed through an overhead $40 \text{ cm} \times 40 \text{ cm}$ quadrat). No differences in these variables were observed among the treatments and therefore these variables were not considered further in analysis.

2.4. Food resources and stomach contents

We determined the composition and spatial distribution of drifting food items available for fish consumption by collecting drift samples at two locations, approximately 100 m and 300 m below the upstream boundary of the study reach. This allowed us to measure the availability of invertebrate and fruit/seed abundance in the drift within the reach section where the enclosures were placed. Drift samples were collected on ten occasions at these two sites throughout the experiment, using $250 \mu\text{m}$ mesh drift nets with $17.5 \text{ cm} \times 17.5 \text{ cm}$ openings set for 24 h. All samples were preserved in 5% formalin in the field, sorted from detritus in the laboratory at $16\times$ magnification, and preserved in 70% ethanol. Aquatic invertebrates were identified to genus or family using Merritt and Cummins (1984). Terrestrial invertebrates were identified to order or genus using Borror and White (1998). Invertebrate length was measured to the nearest 0.05 mm using a binocular microscope equipped with a drawing tube that projected images of invertebrates onto a digitizing pad (Roffand and Hopcroft, 1986). Invertebrate biomass (dry weight) was estimated using published length–weight regressions for aquatic (Meyer, 1989; Benke et al., 1999; Sabo et al., 2002) and terrestrial invertebrates (Edwards, 1966; Sample et al., 1993). Fruits, seeds and fish remains collected in the drift and stomach samples were oven-dried and weighed to the nearest 0.001 g. For the focal species treatments of *C. sanctifranciscense* and *A. lacustris*, we analysed the stomach contents of five fish pairs (i.e., five enclosures) per treatment (N of 5), while for the *H. malabaricus* focal species, we analysed the stomach contents of all four fish pairs (i.e., four enclosures) per treatment (N of 4).

2.5. Diet overlap between individuals

We calculated an index of diet overlap to serve as a measure of intra- and interspecific diet variability. Using the software ecosim v7.2 (Gotelli and Entsminger, 2001), Pianka’s overlap index (Pianka, 1973) was calculated between pairs of individuals in the enclosures as a function of the biomass percentages:

$$\theta_{12} = \frac{\sum_{i=1}^L P_{i2} * P_{i1}}{\sqrt{\sum_{i=1}^L (P_{i2}^2) * (P_{i1}^2)}}$$

where P_{i2} is the biomass percentage of item i in the diet of individual 2 and P_{i1} is the biomass percentage of item i in the diet of individual 1. The mean diet overlap was determined for all focal species treatment combinations, which permitted an evaluation of the degree of diet similarity as a function of the treatment (i.e., same species, same trophic function or different trophic functions). The values of Pianka’s overlap index range from 0 (no diet overlap, high variability) to 1 (complete overlap, no variability). In general, an index value of 0.6 or higher indicates similarity of the feeding niche (Linton et al., 1981).

2.6. Behavior

As higher competition for resources may affect individual behavior and ultimately growth (Vøllestad and Quinn, 2003), we measured two behavioral modalities that included the number of feeding attempts and the number of aggressive interactions performed by fishes. We randomly chose six (4 for *H. malabaricus*) replicate enclosures per treatment combination for the behavioral observations. Feeding attempts were defined as directed pecking motions on the surface, the substrate or the water column. Aggressive interactions were defined as pecking motions or charges directed toward the other individual in the enclosure. The behavioral observations were conducted in blocks of 15 min by

a single observer who snorkeled downstream of each enclosure, as described in Leduc et al. (2010).

2.7. Statistical analysis

To test for a relation between individual scope for growth (i.e., Weatherley and Casselman, 1987) and initial mass, we performed a linear regression of the total increase in biomass as a function of initial mass at stocking. The normality of the residuals was assessed with a Durbin–Watson test. We then assessed whether differences in growth index, dietary overlap, biomass of food resources consumed and behavior occurred between treatments (i.e., same species, similar trophic function, different trophic functions) and between focal species. To compare growth between focal species and treatments, we used a nested analysis of variance (ANOVA) under which the variable ‘treatment’ was nested within the variable ‘species’. We used initial mass as a covariate given it allowed us to control for differences in weight between focal species. Data were log-transformed to respect assumptions of normality. To test for differences in dietary overlap, food resources consumed and behavior, analyses of variances were performed, nesting ‘treatments’ into ‘species’ and considering both variables as random effects. When a significant effect of focal species or treatment was found, we further compared main effect treatments levels using a Tukey HSD test for post-hoc comparisons.

To determine whether a significant relationship existed between trophic complementarity and EF (i.e., fish growth), we calculated an index of function based on growth rate and then regressed it against an index of complementarity (Pianka’s dietary overlap) for the 9 treatments (3 species combinations X 3 treatments). For each treatment (i.e., same species, similar trophic function and different trophic functions) we used a dimensionless growth index (GI) to calculate the relative growth of focal and companion species as the natural logarithm of the ratio of growth in companion species treatments to growth in the focal ‘same species’ treatments; $GI = -\log(N_T/N_O)$, where N_T = growth in companion species treatments and N_O = growth in focal ‘same species’ treatments, after Cooper et al. (1990). The ‘same species’ treatment growth index was assigned a value of 0 (i.e., $\log(N_T/N_O) = \log(N_O/N_O) = 0$). Finally, to provide a basic indication on the type and abundance of drifting food items (i.e., invertebrates, fruit and seeds), we compared the overall biomasses of food items sampled in the drift, the abundance of aquatic or terrestrial items in the drift (hereafter termed ‘origin’) and the number of most abundant invertebrate taxa (>3% of total biomass) between two sampling locations that were separated by ~200 m. The average daily biomass data for the drifting food items were log-transformed to conform to assumption of normality, and we performed paired *t*-test for comparisons between the two drift sampling locations. However, the origin of food items along with the number of abundant taxa remained highly non-normally distributed despite transformation (i.e., Kolmogorov–Smirnov test; $P < 0.001$). We thus used non-parametric Chi-square and Fisher’s exact test for comparisons between sampling locations on these later two variables, respectively. The alpha value was set at 0.05. SPSS version 21 was used for statistical analyses.

3. Results

3.1. Growth

Four replicates were lost during the experiment as a result of fish death: one ‘same species’ treatment of *Cichlasoma* and one in each of the *Astyanax* treatments. Overall, we found a significant effect of the initial mass on absolute growth (Linear regression, $R^2 = 0.45$, $P = 0.01$; ANOVA, $F_{(1,67)} = 17.28$, $P = 0.001$), suggesting that

scope for absolute growth is inversely proportional to individual initial size. No significant difference in the initial mass for a given focal species was found between treatments (univariate analysis of variance, $F_{(1,68)} = 0.25$, $P = 0.776$). Using initial mass as a covariate to remove size effects on growth, we observed a significant effect of the functional treatments on the growth of focal species (nested analysis of variance; $F_{(6,57)} = 5.29$, $P = 0.0002$), along with a significant effect of initial mass ($F_{(1,57)} = 20.18$, $P = 0.0001$). However, difference between focal species appeared to have no significant effect on growth (nested analysis of variance; $F_{(2,7)} = 0.51$, $P = 0.621$). A Tukey HSD test revealed no difference in growth between the ‘same species’ and ‘similar function’ treatments, while the ‘different function’ treatment led to significantly higher growth than either of the two other treatments (for comparison significance at the 0.05 level). For the focal species considered individually, higher growth occurred under the ‘different trophic functions’ treatment when compared to the other two treatments (Fig. 1), although these differences were not statistically significant.

The mean growth index (GI) was negatively related to dietary overlap (linear regression, $R^2 = -0.802$, $F_{(1,8)} = 28.38$, $P = 0.001$),

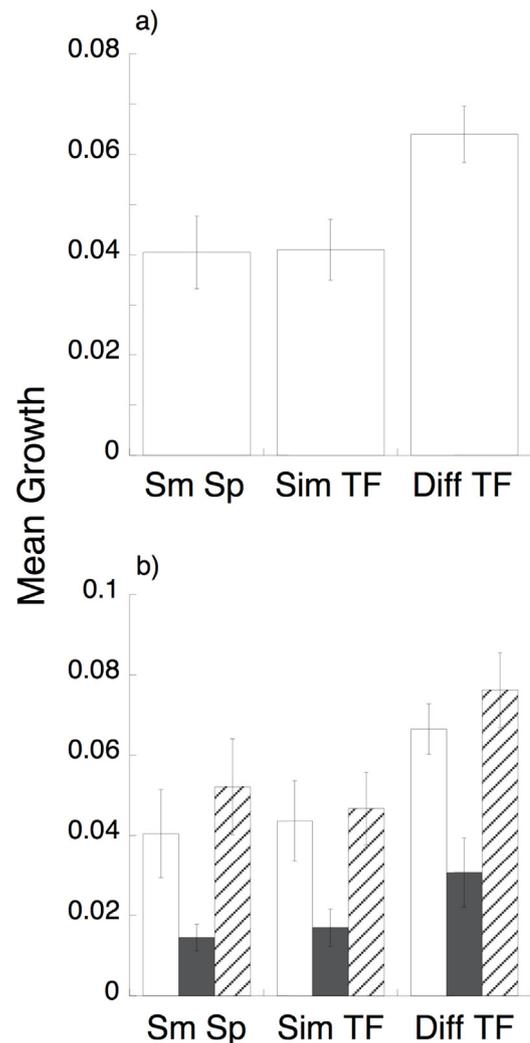


Fig. 1. Growth (final mass–initial mass/initial mass; mean \pm SE) for all three focal fish species in the different treatments (a) and growth of individual focal fish species (b). Focal species, *Cichlasoma sanctifranscense*, *Hoplias malabaricus* and *Astyanax lacustris* are represented by open, grey and diagonally striped bars, respectively. Sm Sp = same species, Sim TF = similar trophic function, Diff TF = different trophic function.

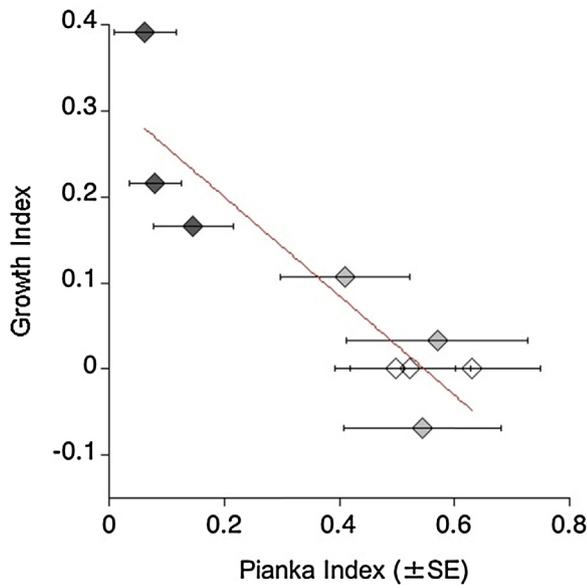


Fig. 2. Relationship between changes in ecosystem function, measured using a growth index (GI), and diet overlap, according to the Pianka Index (\pm SE) between fish pairs of 'same' and 'different trophic function' treatments, measured against 'same species' treatments for each respective focal species. Open, light-gray and dark-gray symbols indicate the treatments 'same species', 'similar trophic function' and 'different trophic functions', respectively.

indicating a strong effect of trophic dissimilarity (i.e., complementarity) on growth (Fig. 2). Higher trophic divergence, as demonstrated by lower dietary overlap, appeared to have promoted EF, while dietary overlap had the opposite effect.

3.2. Food items and availability

The average total daily biomasses of drifting food items were 126.3 mg ($SE \pm 48.11$) and 81.3 mg ($SE \pm 32.6$) for the upstream and downstream sites, respectively, which were not significantly different (paired *t*-test, $T = 1.031$, $P = 0.329$). There was a statistical difference in the percentage of invertebrates of aquatic vs. terrestrial origins between the upstream and downstream collection sites ($\chi^2[1] = 25.45$, $P < 0.001$). At the upstream sample site,

31.2% of the invertebrates were of aquatic origin and 68.3% were of terrestrial origin, while at the downstream site, 52.3% were of aquatic origin and 47.7% were of terrestrial origin. However, the diversity in the number of taxa constituting 3% or more of the total biomass did not statistically differ between the two sampling sites (7 vs. 8 for upstream and downstream sampling site, respectively; Fisher's exact test, $P = 0.381$). Although the total average biomass in the drift was similar between the upstream and downstream sites, the identity of the most abundant taxa noticeably differed (Fig. 3).

3.3. Dietary overlap and stomach content

Functional treatments had a significant effect on dietary overlap and stomach content biomass of enclosed fish pairs (nested analysis of variance; $F_{(6,33)} = 3.061$, $P = 0.017$ and $F_{(6,47)} = 3.319$, $P = 0.008$, respectively). However, neither dietary overlap nor stomach content biomass significantly differed as a function of focal species used (analysis of variance; $F_{(2,6)} = 0.067$, $P = 0.936$ and $F_{(2,6)} = 4.702$, $P = 0.057$, respectively). Tukey HDS post-hoc tests on the dependant variables 'dietary overlap' and 'mean biomass of stomach content' revealed significant difference between 'different trophic functions' and both 'same species' and 'similar trophic function' ($P < 0.01$), while no difference between the latter two treatments could be found ($P > 0.05$; Table 2).

3.4. Behavior

For all species combined, we detected a significant effect of functional treatment on the mean number of aggressive interactions (nested analysis of variance; $F_{(6,45)} = 2.384$, $P = 0.044$), whereby fewer aggressive interactions occurred under the 'different trophic functions' treatment (Fig. 4). However, difference associated with focal species was marginally non-significant for this behavior (analysis of variance; $F_{(2,6)} = 3.866$, $P = 0.083$). No significant difference in the mean number of feeding attempts was detected among treatments (nested analysis of variance; $F_{(6,45)} = 0.569$, $P = 0.753$) or between focal species (analysis of variance; $F_{(2,6)} = 4.370$, $P = 0.067$). Considering *C. sanctifranciscense* and *A. lacustris* individually, feeding attempts for the 'different trophic functions' treatment were elevated relative to the other two treatments, although these differences were not significant.

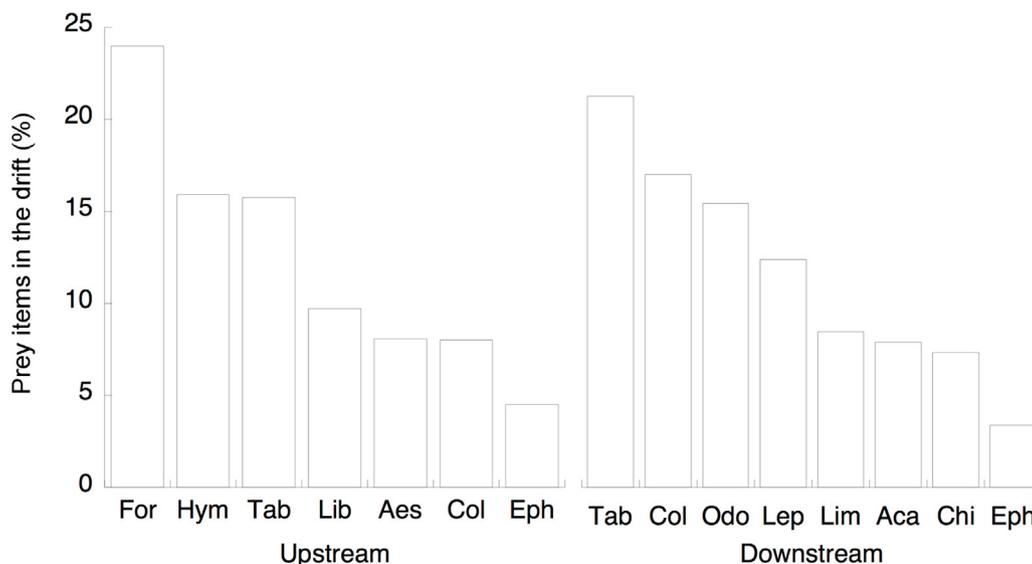


Fig. 3. Distribution of drift biomass among different invertebrate taxa at the upstream and downstream sampling sites. Aca = Acaridae, Aes = Aeshnidae, Chi = Chironomidae, Col = Coleoptera, Eph = Ephemeroptera, For = Formidae, Hym = Hymenoptera, Lep = Lepidoptera, Lib = Libellula, Lim = Limnephilidae, Odo = Odonata, Tab = Tabanida.

Table 2

Diet overlap of focal species using the Pianka Index (bold \pm SE) and mean stomach content biomass (mg, italics \pm SE) of focal fishes for the different treatments. A value of 1 indicates complete diet overlap, while lower values indicate less similarity in feeding niche.

| Treatments | <i>C. sanctifranciscense</i> | <i>H. malabaricus</i> | <i>A. lacustris</i> |
|----------------------------|------------------------------|-----------------------|---------------------|
| Same species | 0.63 (0.11) | 0.49 (0.17) | 0.50 (0.09) |
| | <i>3.19 (0.58)</i> | <i>9.85 (3.28)</i> | <i>2.02 (0.38)</i> |
| Same trophic function | 0.57 (0.15) | 0.54 (0.21) | 0.46 (0.20) |
| | <i>4.03 (1.17)</i> | <i>10.53 (4.50)</i> | <i>3.70 (1.51)</i> |
| Different trophic function | 0.08 (0.04) | 0.26 (0.12) | 0.14 (0.16) |
| | <i>7.44 (2.37)</i> | <i>23.23 (5.76)</i> | <i>7.21 (7.29)</i> |

4. Discussion

Our experiment provides evidence that taxonomic diversity is a less important driver of energy transfer into secondary production (fish growth) than trophic diversity in the stream-fish assemblage studied. This finding is consistent with earlier studies in which functional richness and diversity were found to be stronger determinants of ecosystem process rates than total species number (Tilman et al., 1997b; Fornara and Tilman, 2008; Fox and Bellwood, 2013). While these studies demonstrated that higher EF was associated with higher complementarity (i.e., lower overlap) in resource use, studies providing definitive insights into the specific mechanisms whereby diversity facilitates EF for organisms with complex suites of biological responses are rare.

In this study, we show that higher functional heterogeneity led to reductions in the overlapping use of dietary resources (Fig. 2) and this resulted in higher EF in terms of fish biomass production (Fig. 1). When comparing growth within a single functional feeding guild, we found no significant differences between species pairs, regardless of their taxonomic identity. This suggests that species identity is not as important as functional identity, at least within the Água Azeda fish community. This conclusion is supported by the observation of higher diet overlap and lower food intake when the focal and companion species had either the same identity or were within the same functional guild. By contrast, lower dietary overlap and higher food intake were associated with heterogeneity of function within fish pairs, rather than species diversity *per se*.

Clearly, complementarity in resources utilization may occur on different niche-spaces axes (Rosenfeld, 2002; Wojdak and Mittelbach, 2007; Carey and Wahl, 2011). Our rationale for assessing complementarity of dietary resources pertains to the fact that freshwater trophic chains are typically linear (more so than both terrestrial and marine ecosystems; Shurin et al., 2002; Thompson et al., 2007) such that trophic interactions are likely to have dominant effects. While in our experiment we focused on dietary

complementarity, we did not measure spatial partitioning. Carey and Wahl (2011) tested complementarity in 1325-L tanks mesocosms and found that spatial partitioning among fish species promoted EF, whereby fish production under species-rich treatments was highest as a consequence of lower spatial overlap. High habitat homogeneity in Água Azeda Creek (i.e., absence of pool-riffle sections and uniform sand substratum) and its shallow depth (average <20 cm) likely reduced the importance of spatial partitioning relative to dietary partitioning, particularly in the smaller stream enclosures we used when compared to the mesocosms tanks of Carey and Wahl (2011) experiment. Moreover, within Água Azeda Creek, food resources appeared relatively homogeneous in terms of biomass and in the number of abundant species, as these variables did not differ statistically when measured several hundred meters apart (Fig. 3). Such apparent homogeneity in both habitat complexity and food resources distribution suggests that spatial partitioning may be a driver of lesser importance on EF than dietary partitioning associated with different trophic guilds.

While our results point to the importance of trophic functional diversity over species diversity, other studies have found that species identity rather than species or functional richness significantly affected EF (Downing and Leibold, 2002; Downing, 2005). In Downing (2005), functional group biomass (grazers and invertebrate predators) responded to both functional group diversity and species composition within functional groups. This effect may have resulted from low interspecific niche overlap (high functional distinctiveness, even within a functional group) promoting EF. However, the results of other studies (i.e., Heemsbergen et al., 2004; Duffy et al., 2007; Fornara and Tilman, 2008) suggest, as do the results of our study, that greater functional differences occur between species belonging to different guilds than between species within a guild.

Just as the degree of resource partitioning may affect complementarity, overlap in resource requirement may either accentuate (i.e., through facilitation) or depress (i.e., through competition) EF. Facilitation is argued to contribute to EF (Cardinale et al., 2002) while competition may have the opposite effect through exclusion or antagonistic interactions (Vøllestad and Quinn, 2003). Indeed, we showed that the increased resource partitioning under high functional diversity treatments led to a reduction in antagonistic responses between fish pairs (Fig. 4). Reduced aggression is likely a consequence of reduced overlap in dietary resources and space use between focal and companion species (although in our experiment, spatial habitat use was only assessed qualitatively). Unlike the focal species, which are generalist water-column/surface feeders, *Hoplosternum littorale* (used in the 'different trophic functions' treatments) is typically a

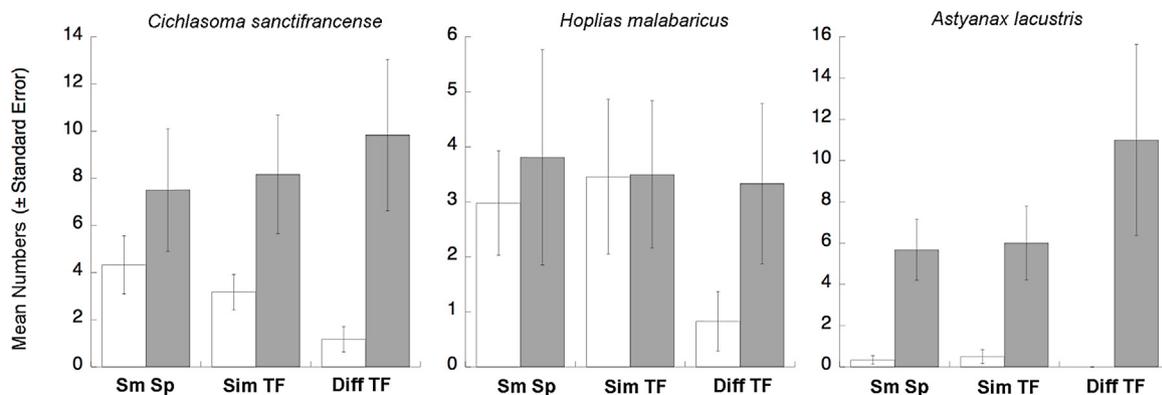


Fig. 4. Mean number (\pm SE) of aggressive interactions (open bars) and feeding attempts (dark bars) by the three focal species. Sm Sp = same species, Sim TF = similar trophic function, Diff TF = different trophic functions.

benthic detrital and invertebrate forager (Mérona and Rankin-de-Mérona, 2004; Luz-Agostinho et al., 2006). Functional distinctiveness in resources used between fish pairs likely contributed to reducing direct competition that furthered EF. Although *H. malabaricus* may be argued to display benthopelagic feeding behavior (Luz-Agostinho et al., 2006), spatial segregation with *H. littorale* may have contributed to increased complementarity and EF, as evidenced by the highest growth being observed for *H. malabaricus* in the 'different trophic functions' treatment (Fig. 1b). Contrary to our expectations, however, we did not observe significantly greater levels of facilitation (i.e., increased feeding rates) among distinct trophic function treatments. Although our statistical power to detect this potentially subtle effect might have been limited by our sample size, we observed increased feeding attempts in 2 of 3 focal fish species under the 'different trophic functions' treatment.

The Brazilian Atlantic forest is one of the world's hotspots for biological diversity, and both aquatic and terrestrial ecosystems in this region have been extensively fragmented and degraded (Myers et al., 2000; Estavillo et al., 2013). While many tropical watersheds have high species diversity (beta and gamma) over large geographic ranges (Mazzoni et al., 2006), local species diversity and particularly functional diversity may remain low (Gerhard et al., 2004; Mazzoni et al., 2006). Under these circumstances, the loss of a single trophic functional group may have significant consequences for EF. Taylor et al. (2006) demonstrated that overharvesting a unique yet abundant fish species (*Prochilodus mariae*) displaying singular and non-redundant trophic function at the community level may affect important ecosystem processes in tropical streams, underscoring the ecosystem consequences of functional diversity loss. This may be especially true when low within-guild species diversity is combined with limited functional redundancy. For instance, the loss of an entire functional group because of climatic shifts or disturbances, which tend to affect certain groups more than others, may have a larger impact on EF than would random species extinctions (McIntyre et al., 2007). The extent to which ecological functions change following extinction depends greatly on which biological traits are extirpated (Hooper et al., 2005). Presumably, the local extirpation of *H. littorale* from the studied stream would have implications on community-wide biomass fish production if, as our results suggest, dietary resource overlap and competitive interactions are strong.

Our experimental design has several limitations that must temper the interpretation of results. Although replication of multiple taxa within each functional group would have been desirable, a limited pool of abundant species prevented replication of different species within each functional group. Without such complete functional replication, we used 6 of 10 fish species that were present in the Água Azeda Creek, while unused taxa were relatively rare (A.O.H.C.L., personal obs.). Similarly, species replication within guilds and the trophic guilds treatments were limited and not randomly selected. These design constraints were imposed by the limited number of abundant species present in the local species pool and logistical limits on the number of enclosures that could be installed and maintained. Nevertheless, we would argue that the results are robust and have some generality under conditions of relatively low species and functional diversity, which are frequent in the tropics and even more so in temperate zone streams. Furthermore, because the species chosen were both sympatric and abundant in their community, their interactions likely play a dominant role in local ecosystem dynamics. These also represent common functional groups in tropical and temperate streams, such that the underlying mechanisms of functional differentiation and complementarity are likely to be general.

One potential limitation with stream enclosure experiments is that enclosure mesh sides may act as a barrier to larger prey items,

leading to differences in invertebrate densities between enclosures and unmanipulated habitat, causing unrealistic results (*sensu*, Englund and Olsson, 1996). However, Zimmerman and Vondracek (2006) demonstrated that the presence of invertebrates inside stream enclosures was not significantly affected by a mesh size as small as 3 mm, suggesting that the 7 mm mesh size that we used should have had minimal effects on invertebrate densities. For instance, an invertebrate length:width ratio of 5 (typical for prey items like mayflies or dipteran larvae) would allow exchange of benthic prey up to 3.5 cm long through enclosure walls. By contrast, the propensity of larger detrital matter to pass through the enclosure mesh is likely more limited and potentially affected growth and/or behavior of *H. littorale*, the detritivore–benthivore species we used in the 'different trophic function' treatment. It is unknown if detrital matter and benthic invertebrates were reduced to a level that affected the growth and/or behavior of *H. littorale*, compared to natural conditions. However, as no *H. littorale* individual was lost while in captivity and we observed seemingly normal feeding behavior during the experiment, we would argue that enclosure conditions remained within boundaries that provide ecologically-relevant results.

The period under which this experiment was conducted may directly affect the strength of our results. Indeed, we conducted this experiment in the dry season due to the logistical constraints of using stream-enclosures when rainy season spates are frequent, along with the rationale that the dry season months represent the period of maximum biotic control. Under the high water-discharges that characterises the rainy season, abiotic control of the ecosystem is likely far more important than species interactions. Thus, the strength of species interactions as well as functional and taxonomic effects on EF may be dependent on environmental settings.

The venue under which experiments are conducted may likewise modify interactions strength between species (Skelly, 2002). While use of species from a natural fish assemblage embedded in their natural habitat represents more realistic conditions than many laboratory microcosms, it remains possible that the effects measured in enclosures may not represent their magnitude under fully natural conditions. Conducting species and/or functional group removal at the stream-reach scale (*sensu*, Taylor et al., 2006) is clearly the next step in predicting the effect of diversity on EF and fish productivity at the assemblage level.

Interest in assessment of the role of biodiversity on EF has been justified on the grounds that the loss of biological diversity ranks among the most pronounced changes to the global environment and that reductions in diversity and corresponding changes in species composition could alter fluxes of energy and matter that underlie important services that ecosystems provide to humanity (e.g., the production of food; Holmlund and Hammer, 1999; Díaz et al., 2006). The results of our study indicate that complementarity of resource use is a primary cause of enhanced EF and confirm that the loss of EF (in terms of fish biomass production) is likely to be greatest following the loss of functionally distinct species in low-diversity assemblages. The importance of diversity as it relates to not only species richness but also functional richness is underscored here. This may be particularly important for freshwater fish communities, which are often depauperate and in which monospecific functional groups are common and often locally or regionally depleted through harvest fisheries.

Additionally, a suite of mechanisms beyond direct exploitative effects may influence EF, including direct (i.e., competition) and indirect (i.e., facilitation) interactions. Under these conditions, the maintenance of fish biomass production requires a thorough assessment of species identity and their functional attributes on the niche-space axes of greatest potential importance (Gamfeldt et al., 2008). Such functional assessment is fundamental to

identifying the species most likely to increase functional heterogeneity, which may in turn both broaden community-wide resource use and promote behavioral responses that increase resource use efficiency.

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