Understanding the role of interactions in influencing community structure and ecosystem function is a goal in ecology, and identifying biotic entities that are strong interactors is imperative for setting targeted conservation strategies. Several different mechanisms have been linked with strongly interacting species (e.g., predation, competition, abiotic habitat modification), but the most important organisms often influence ecosystems in multiple ways. We propose that these strong interactors share a broad common feature: They catalyze ecosystem processes, such as rates of primary productivity, species interactions, and/or physical disturbances. We provide a case study of Spanish cedar (*Cedrela odorata*), focusing on its influence as a provider of large woody debris (LWD) on food web dynamics in tropical floodplain rivers and associated oxbow lakes. Large woody debris has been subject to considerable attention because of its perceived importance in creating geomorphologically favorable conditions for target commercial species (e.g., distribution of pools and riffle for salmonids). However, in this study we suggest that LWD catalyzes a suite of ecological processes in addition to geomorphology that determines its important role within aquatic communities. Through a factorial experiment manipulating large and small fish access to treatments with and without LWD piles, we tested the role of Spanish cedar in modifying interactions between different-sized fishes, invertebrates, and primary producers in a tropical floodplain river and associated oxbow lake. Path analysis revealed that fishes influence particulate matter accumulation and invertebrate abundances more so in wood piles than outside of wood piles in both river and lake ecosystem contexts. In addition to providing the first experimental test of factors controlling trophic dynamics in an Amazonian river, we suggest that understanding the role of organisms through the ecological processes they catalyze provides an overarching conceptual framework to link single species and ecosystem-based management strategies.

**Key words:** Amazon; bottom-up; ecosystem engineers; food webs; foundation species; keystone species; large woody debris; Neotropical rivers; primary production; process catalyzers; strong interactors; top-down.

**Received** 6 July 2017; revised 27 October 2017; accepted 30 October 2017. Corresponding Editor: Robert R. Parmenter.

**Copyright:** © 2018 Heilpern and Wootton. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

1 Present address: Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, New York 10027 USA.

† E-mail: s.heilpern@columbia.edu

**INTRODUCTION**

While abiotic factors and energetic constraints are fundamental in structuring communities and ecosystems, interactions between species can play equally central roles. Individual species, or groups of functionally similar species, can alter the amount of material and energy within an ecosystem and, consequently, the abundance and diversity of other organisms (Elton 1927, Paine 1966). Since Paine’s (1969) seminal work, ecology has accrued many examples, from a variety of
terrestrial and aquatic ecosystems, of individual species, or groups of functionally similar species, that are important in determining community structure and ecosystem function through their strong interactions (Estes et al. 1998, Alvarez-Filip et al. 2009). These strong interactors affect ecosystems via multiple trophic and non-trophic interactions, and understanding how they influence the abundance and diversity of organisms and ecosystem function in different ecosystem contexts is a goal in ecology and imperative for linking single species and ecosystem-based conservation strategies.

The keystone species concept is perhaps the most ingrained example of individual species that play large roles in structuring communities (Paine 1966, 1969). These species have a disproportionately large impact on a community or ecosystem relative to their low abundance or biomass, typically through trophic interactions (sensu Power et al. 1996). However, species can also influence communities through non-trophic pathways, such as by transforming the physical environment and modifying available habitat. Ecosystem engineers are those organisms that control the availability of resources to other organisms by modifying the abiotic environment (Jones et al. 1994). In contrast to these well-defined concepts, foundation species as a term has been applied less liberally (Angelini et al. 2011). Originally defined by Dayton (1972) as those species that have a large role in defining the structure of a community, including by determining spatial habitat, energy provisioning, and competitive hierarchies, extensive usage of similar terms (e.g., autogenic ecosystem engineer, dominant species; reviewed in Angelini et al. 2011) has obscured the concept. Although identifying these strongly interacting species has become a central theme of modern ecology and conservation, their broad and often overlapping definitions have precluded the formulation of a general framework to guide their application.

Although different ecological constructs, keystones, ecosystem engineers, and foundation species share important commonalities, they all recognize that certain species can have large effects on others through their influence on local abiotic and biotic factors. Distinguishing between the three, however, has been problematic. For example, reef-building corals have been variously termed foundation species (Alvarez-Filip et al. 2009), ecosystem engineers (Foster et al. 2012), and keystone species (Shinzato et al. 2011). Shinzato et al. (2011) and Foster et al. (2012), for example, focused on the physical shapes, or architectural complexity, as the factor responsible for the large community impacts of coral species. In addition to structure, however, high primary production and food availability on reefs attract numerous consumers, including large groups of fish, which can, in turn, lead to locally concentrating nutrients as well as altering trophic dynamics (Meyer et al. 1983, White and O’Donnell 2010, Allgeier et al. 2013). Unlike a cascade, this catalysis of processes involves the simultaneous direct modification of rates of trophic and non-trophic interactions, and parsing out the relative strength of these interactions is challenging because of the potential for feedback loops between these interacting axes. Nevertheless, the keystone species, ecosystem engineers, and foundation species concepts do not consider the potential for a given species, or functionally similar group of species, to leverage its importance in the community by altering multiple pathways simultaneously. By forcibly classifying species into one or more of these concepts, other important mechanisms may be overlooked.

In aquatic ecosystems, riparian tree species generate large woody debris (LWD), which plays important roles in structuring communities and influencing ecosystem function (Montgomery et al. 1996, Stewart et al. 2009). Like coral, LWD is heterogeneously distributed across the landscape, and woodpiles can be areas of high primary and secondary productivity in relation to the surrounding matrix (Benke et al. 1984). Fish also respond positively to the abundance of LWD and aggregate around woodpiles in both stream and lake ecosystems (Schindler et al. 2000, Langford et al. 2012). The positive response of multiple trophic levels is typically attributed to the effect of LWD on geomorphological characteristics (e.g., habitat structure, flow, and sedimentation; Montgomery et al. 1996, Stewart et al. 2009). Given the increase in productivity on LWD, however, some authors have also suggested that trophic interactions and resource concentration mechanisms underlie the positive impacts of LWD on communities (Wright and Flecker 2004, Pettit et al. 2013). Although natural
resource managers have focused on the impact of LWD distribution on fishes because of its perceived importance in creating favorable conditions for target commercial species (e.g., salmonids; Montgomery et al. 1996, Stewart et al. 2009), few studies have experimentally manipulated LWD to mechanistically test its multiple effects on river and lake ecosystems (Cederholm et al. 1997, Roni and Quinn 2001). Further, given the focus of geomorphology, few authors have identified LWD as a biotic entity that affects the rates of multiple community and ecosystem processes.

As in temperate systems, wood is heterogeneously distributed in tropical rivers and lakes, and woodpiles can be areas of high primary and secondary aquatic productivity (Pyron et al. 1999, Cadol and Wohl 2010). Fish respond directly to the distribution and abundance of LWD (Bojesen and Barriga 2002, Wright and Flecker 2004, Willis et al. 2005); however, the mechanisms underlying the responses may differ among ecosystems. Neotropical fishes, for example, are functionally diverse, and grazers—benthic feeders that consume algae and detritus—are especially important in structuring communities and influencing ecosystem function (Wootton and Oemke 1992). Grazing fishes do so by influencing algal standing crops (Power 1990, Flecker 1996), reducing sediment accumulation and transport (Taylor et al. 2006), and creating biogeochemical hotspots (McIntyre et al. 2008). These effects are most apparent for larger grazers on hard substrates rather than on the sandy bottom of large rivers (Forsberg et al. 1993, Winemiller et al. 2014). Through these interactions, highly diverse tropical fish assemblages impact food webs and indirectly reduce secondary production (Hall et al. 2011, Winemiller et al. 2014). Thus, as in temperate systems, rather than acting solely like a keystone, ecosystem engineer, or foundation species, riparian trees, through their introduction of LWD into aquatic ecosystems, may catalyze a suite of ecological processes through their independent impact on members of different trophic levels (e.g., primary producers, invertebrates, grazing fish).

In this study, we explore how riparian trees, by introducing LWD in tropical rivers and lakes, can be process catalyzers because they simultaneously modify interaction rates between different trophic levels, thus influencing community structure and ecosystem function. More specifically, we asked whether woody debris mediates trophic dynamics between fish, primary producers, organic matter accumulation, and aquatic invertebrates. By employing a coupled approach, including surveys and field experiments in ecosystems with different characteristics, we parsed out the multiple roles of LWD in modifying interactions between fish, primary resources, and invertebrates in a Neotropical floodplain river and associated oxbow lake. Particularly, we hypothesized that the interaction between fishes and detrital sediment accumulation and invertebrate densities is stronger on substrates placed in woodpiles than those placed outside of woodpiles in both ecosystem contexts. In contrast to the prevailing notion that LWD is important in aquatic systems because of its effect on stream geomorphology, these results suggest that Spanish cedar, as a provider of LWD, can be a biotic entity that catalyzes biological processes that are central to the organization of tropical freshwater ecosystems.

**Methods**

**Description of the study site**

The Manu River, situated within the Manu National Park (MNP), originates at the foothills of the Andes and drains a protected area of 19,000 km² in the Madre de Dios Department in southeastern Peru. The river is a low-gradient floodplain whitewater tributary of the Madeira River, itself a tributary of the Amazon River, and is associated with over 30 oxbow lakes. The Manu is an actively meandering river that experiences channel avulsions at an approximate rate of two per decade, which is when the oxbow lakes form (Osorio et al. 2011). The basin receives an average yearly precipitation of 2300 mm/yr. There is a pronounced dry season lasting from May to October, which is when channels connecting the river to the oxbow lakes and many adjacent swamps and wetlands dry up, and large sandbanks become exposed along the river.

The main study site is adjacent to the Cocha Cashu Biological Station (11°56′ S, 71°24′ W) at an elevation of approximately 300 m above sea level. At this remote location, river width is approximately 150 m and depth on average is 1.2 m (Belcon 2012). Given the meandering nature of the river, during the dry season there are...
depositional areas where LWD tends to aggregate, such as at river bends, and other areas where the presence of wood is periodic. Riparian vegetation is a primary contributor of LWD into aquatic ecosystems, and the composition of LWD in the river and lake reflects the process whereby the river meanders and erodes terrestrial habitats. Although there are over 600 tree species in the region, LWD species composition is dominated by only a handful of species, which reflect the vegetation of riparian zones (M. Silman unpublished data). Particularly, within the park’s boundaries, Spanish cedar (Cedrela odorata; Meliaceae) is highly abundant in both riparian habitats and in LWD piles. This is in stark contrast to outside the park where Spanish cedar has been heavily exploited prompting its listing as vulnerable by the IUCN.

Over 210 fish species have been recorded in the Manu River, and over 80 fish species in the Cocha Cashu Lake (Ortega et al. 2012), with fish assemblages dominated by Characiformes (tetras and allies) and Siluriformes. Because of the high diversity, as in several other Amazonian piedmont rivers, the trophic composition of aquatic communities is not easily described (Flecker 1996). However, bottom-feeding is a common strategy, and grazing fish—benthic consumers of algae and detritus—are widespread. Of the grazing fish, armored catfish (Loricariidae), Prochilodus nigricans (Prochilodontidae), and toothless characins (Curimatidae), which range in body size from 5 to 45 cm, are the most abundant in both the river and the lake (Ortega 1996, Osorio et al. 2011). Other common members of the fish community include small omnivorous characins, including Roeboides sp., Triportheus angulatus, and Knodus sp., as well as small heptapterid catfish. Lastly, in the river, larger long-whiskered catfish (Pimelodidae) and pacu (Colossoma macropomum) are the dominant predators, whereas in the lake, peacock cichlids (Cichla sp.) and red-bellied piranhas (Pygocentrus nattereri) are the most commonly caught predators. Caiman are also abundant in both ecosystems, particularly Melanosuchus niger.

Testing the role of large grazer and small omnivore and insectivore fishes and LWD

Experiments were conducted from 17 August 2014 to 1 September 2014, a period corresponding to the dry season, to disentangle the relative effects of large fish (on average approximately >15 cm; primarily large grazers), small fish (<15 cm; primarily small omnivores and insectivores) and LWD on chlorophyll a concentrations, accumulation of sediment ash-free dry mass (AFDM), and aquatic invertebrate densities in two ecosystem contexts, the main river channel and periodically connected oxbow lakes. In the river, the experiment was factorially designed to manipulate large fish and LWD (large fish exclusion × LWD), with three blocks of five treatments: (1) wood added, large fish excluded; (2) wood absent, large fish excluded; (3) wood added, accessible to large fish; (4) wood absent, accessible to large fish; and (5) cage control (Fig. 1). Additionally, to manipulate small fish, within each treatment, one exposed substrate and one substrate surrounded by a smaller mesh were installed as pairs (Fig. 1C, D).

The exclosure treatments were 8 × 10 m in size, and constructed using 26 m of poultry wire (mesh 2.5 cm) attached to 1.5 m rebar with plastic ties and lodged into the sandy substrate on a sandbank. The cage control was constructed with 8 m of poultry wire and installed to control for the potential effects of altered flow caused by the poultry wire. In addition to the control, the large mesh and size of the cages were purposely employed to decrease the effect of the cage manipulations themselves. To emulate woodpiles, we obtained waterlogged wood from nearby wood deposition sites in the river and distributed pieces among the treatments. Rebar and metal wire were used to support the wood in case a rapid increase in flow was to disturb the piles. To create woodpiles, we primarily used Spanish cedar (C. odorata), a commercially important species common in the Manu River, but heavily exploited in other areas, but supplemented the woodpiles with other species as necessary. Gathered wood was left out in the sun for approximately 48 h and distributed equally among the different blocks and treatments to control for the potential confounding effects of individual pieces of wood.

Within each treatment, we installed 15 × 15 cm paired substrates, constructed out of Spanish cedar. Substrate pairs were installed at roughly the same depth (N = 30, mean depth = 14.07 SE ± 0.68 cm) and included an exposed substrate and a substrate surrounded by a 1-cm mesh cage to prevent access by smaller fish (Fig. 1C, D).
Additionally, because depth is an important factor influencing sedimentation and chlorophyll a concentrations, and because LWD creates substrate elevated off the bottom, in both wood minus exclosure and wood minus open treatments, we installed three substrates at different depths (40, 15, and 1 cm below the water surface; $N = 12$), to explore how LWD might increase periphyton production, and to probe the provision of elevated substrate by LWD.

To test for the effect of LWD piles, fish, and depth in the lake, emulating the same experiment conducted in the river was not possible because of logistical constraints. Thus, we employed a factorial survey design and installed four pairs of substrates (i.e., exposed and caged with a 1-cm mesh) inside and outside of existing wood piles ($N = 16$). Substrates were installed on the same bank side, and at similar distances from the lake bank to control for sunlight and shadows caused by the overhanging vegetation for two weeks (27 August 2014–10 September 2014). All substrates were recovered except one caged substrate from an open lake habitat.

**Measurement of organic matter, chlorophyll a, and invertebrates**

After two weeks, substrates were removed from each plot for analysis. A net (250 µm mesh size) was placed downstream from the substrate to catch drifting invertebrates when dislodging the substrate. Subsequently, substrates were placed in a bucket and set aside for processing. To collect algae and sediment, substrates were gently scrubbed into a known amount of water. This liquid was then homogenized, and a subsample was filtered on pre-ashed filters (Whatman GF/C), sundried in the field for approximately 24 h, and stored with desiccant for later laboratory analysis. Although conventional protocols for measuring
chlorophyll \(a\) concentrations call for freezing samples immediately after collection (APHA 1998). electricity and refrigeration were not available at this remote field site. Despite undergoing some degradation over time, using this method provides a reliable measurement of relative chlorophyll \(a\) concentrations (D. Obrecth and L. C. Davenport, personal communication). The clear expectations of chlorophyll \(a\) levels on substrates installed at different depths also afforded an additional line of evidence to ensure that the relative measurements were reliable. After subsampling the substrate for sediment and algae, the substrate was inspected for remaining attached invertebrates. The remaining water was filtered through a Parker Filter, a 250-\(\mu m\) mesh placed between the lid and the rim of a 1-L plastic storage jar to collect the invertebrates, which were then preserved with 95% ethanol and stored for later laboratory analysis.

In the laboratory, invertebrate densities were obtained by counting individuals to the lowest taxon readily identified, typically family, using Merritt and Cummins (1996). AFDM was obtained by drying a filter at 60°C for 24 h and weighing it, and then combusting the sample at 550°C for 2 h and reweighing it. The difference between the dry and ashed weight was used as an estimate for AFDM accumulation. Chlorophyll \(a\) concentrations were determined by using the overnight 90% ethanol extraction protocol using spectrophotometric methods (APHA 1998).

**Statistical analysis**

We applied path analysis (Grace 2006) to both the river and lake data sets independently to test which hypothesized causal chain of interactions best explains the results. Although natural history knowledge can provide insights as to what causal chain of interactions explain the results obtained, understanding how all variables are related was not possible with our experimental design because not all factors were manipulated (e.g., chlorophyll \(a\), AFDM, invertebrate densities). For example, using simple comparisons of treatments might detect significant differences between substrates in AFDM accumulation and invertebrate densities in both the presence and the absence of LWD. However, pairwise comparisons would not conclusively indicate whether these results were driven by a cascade in which insects were released from top-down control, or whether the increase in invertebrates resulted from bottom-up resource availability effects. Analyzing the whole experiment using traditional ANOVA methodology would not uncover the multiple intertwining mechanisms underlying our results. In contrast, path analysis provided a quantitative examination of the best casual chain of interactions while also taking into account those interactions that were not directly manipulated (Wootton 1994, Grace 2006).

Path analysis was applied by conducting multiple regressions on each response variable (i.e., chlorophyll \(a\), AFDM, and invertebrate densities) determined by a range of different possible causal explanations. These hypotheses were based on previous natural history knowledge and subsequently made more parsimonious by eliminating non-significant interactions in a stepwise manner. Categorical variables (e.g., substrate, LWD, habitat) were converted to a binary scale (1 for presence; or 0 for absence). Because large fish treatment effects were always highly insignificant, a corresponding exogenous variable was eliminated in all path models. Depth, chlorophyll \(a\), AFDM, and invertebrate densities were all log-transformed to meet linearity assumptions. Additionally, given our initial hypothesis, we created an aggregate variable to account for the interaction between LWD and small fish manipulations. The values for this variable were 0, 0, 1, 2, corresponding to LWD(+)-cage, LWD(−)-cage, LWD(−)-exposed, LWD(+)-exposed, respectively. These values were selected given our expectations that the effect of LWD and small fish would be additive and provide a conservative estimate of the combined impact of these two factors. The aggregate variable was treated as an endogenous variable rather than as an exogenous variable, because it was calculated from LWD and cage variables. Since these parent variables were experimentally set, the paths leading to the aggregate variable were defined a priori and did not need to be estimated.

Detailed methods on estimating path coefficients and assessing model fit are discussed in Wootton (1994). Briefly, to assess which hypothesis best described the data, we compared the observed correlation matrix (river: Table 1; lake: Table 2) with that predicted by each path model by using the maximum-likelihood chi-square
Table 1. Observed correlations between variables from the river manipulation experiment.

| Variable | Chla | AFDM | Inverts | WSf | Depth | Sfish | Wood |
|----------|------|------|---------|-----|-------|-------|------|
| Chla     | 1.000  | –0.008 | 0.021  | 0.022 | –0.360 | 0.124 | –0.196 |
| AFDM     | –0.008 | 1.000  | 0.503  | 0.022 | –0.374 | –0.220 | –0.325 |
| Inverts  | –0.021 | 0.503  | 1.000  | –0.692 | –0.211 | –0.628 | –0.086 |
| WSf      | 0.022  | –0.338 | –0.692 | 1.000 | –0.023 | 0.869 | 0.201 |
| Depth    | –0.360 | –0.374 | –0.211 | 1.000 | –0.117 | 0.223 |
| Sfish    | 0.124  | –0.220 | –0.628 | 0.869 | –0.117 | 1.000 | 0.005 |
| Wood     | –0.196 | –0.325 | –0.086 | 0.201 | 0.223  | –0.189 | 1.000 |

Note: Variable codes: Chla, chlorophyll a; AFDM, ash-free dry mass; Inverts, invertebrate densities; WSf, wood–small fish aggregate variable; WF, wood–fish aggregate variable; Depth, substrate depth; Sfish, small river fish; Fish, lake fish; Wood, large woody debris.

Results

By including all variables in one modeling approach, the path analysis revealed the most likely causal connections among the set of manipulated and response variables, thereby providing an illustrative set of insights about the mechanisms driving the observed patterns. The best-fit model for the river indicated that the only variable influencing chlorophyll a was depth ($R = –0.360, P = 0.019$; Fig. 2A, B). Including the aggregate variable improved the fit to explain the relationship between small fish, wood, AFDM, and invertebrate densities ($\Delta AIC = 1.96$). AFDM accumulation on the substrates was negatively influenced by both depth ($R = –0.382, P = 0.016$) and the aggregate variable describing the small fish–wood interaction ($R = –0.347, P = 0.008$). While invertebrate densities were strongly negatively related to the aggregate variable ($R = –0.589, P < 0.001$), AFDM had a positive impact on their densities ($R = 0.304, P < 0.011$). Models that included small fish and wood independently, as well as those including reciprocal effects of invertebrates on chlorophyll a and AFDM, and between chlorophyll a and AFDM performed less well.

The best-fit model for the lake was topologically similar to the river model and included the aggregate variable rather than independent paths between endogenous variables, wood, and fish ($\Delta AIC = 1.690$; Fig. 3A, B). Although chlorophyll

Table 2. Observed correlations between variables from the lake manipulation experiment.

| Variable | Chla | AFDM | Inverts | WSf | Depth | Sfish | Wood |
|----------|------|------|---------|-----|-------|-------|------|
| Chla     | 1.000  | –0.016 | 0.005  | 0.012 | 0.071 | –0.196 | –0.360 |
| AFDM     | –0.016 | 1.000  | 0.804  | 0.012 | –0.482 | –0.096 | –0.096 |
| Inverts  | 0.005  | 0.804  | 1.000  | –0.748 | –0.532 | 0.005  | 0.124 |
| WSf      | –0.131 | –0.748 | –0.532 | 1.000 | 0.234  | 0.005  | 0.005 |
| Depth    | –0.482 | 0.023  | 0.154  | 0.234 | 1.000  | 0.005  | 0.005 |
| Sfish    | 0.096  | –0.890 | –0.734 | 0.899 | 0.016  | 1.000  |
| Fish     | 0.012  | 0.092  | 0.259  | 0.257 | 0.662  | –0.071 |
| Wood     | 0.124  | –0.071 | 0.734  | 0.662 | 1.000  |

Note: Variable codes are the same as in Table 1.
a had a marginally significant positive association with the presence of wood ($R = 0.590, P = 0.066$), the final model only included the negative effect of depth, as in the river model ($R = -0.482, P = 0.069$). AFDM, in contrast, was negatively influenced by the aggregate variable ($R = -0.748, P = 0.001$), but not by depth. Invertebrate densities were strongly associated with the fish–LWD interaction variable ($R = -0.532, P < 0.05$), but not directly influenced by chlorophyll $a$, fishes, or wood. However, this model was statistically indistinguishable from the next best performing model, which included a direct path between AFDM and invertebrate densities rather than a path between the fish–LWD interaction variable and densities ($\Delta AIC = 0.825, R = 0.804, P < 0.001$). As in the river, models that included reciprocal effects of Chl$\alpha$ on AFDM and/or invertebrates performed less well.

**DISCUSSION**

Path analysis revealed that LWD had an indirect impact on the river and lake food webs due to its interaction with fishes to determine AFDM accumulation and invertebrate densities. In the river and lake experiments, the interaction between LWD and small fishes influenced the strength of top-down control of AFDM and invertebrates. These findings provide the first experimental evidence of the indirect trophic effects of LWD in two different Amazonian freshwater ecosystem contexts and support the notion that LWD plays a short-term role in structuring community dynamics and ecosystem attributes by catalyzing the strength of bottom-up and top-down interactions.

Accumulating evidence suggests that rather than being treated as constant, interaction rates

---

**Fig. 2.** Path diagrams depicting the two best-fit models in the river. All variables with prefix $l$ were log-transformed. Thick arrows represent statistically significant ($P < 0.05$) paths from multiple regression analysis. Path coefficients are presented adjacent to paths. Total variance explained for each endogenous variable is presented in parenthesis. The $R^2$ represents the fit between the observed and predicted correlation matrix. (A) River hypothesis 1 (RH1); (B) river hypothesis 2 (RH2).
are context-dependent and, in particular, the presence of other biotic entities can alter the magnitude, direction, and distribution of interactions across ecological networks (Wootton 1993, Peacor and Werner 1997, Trussell et al. 2002). The effects of LWD as a geomorphological force shaping aquatic communities and affecting ecosystem processes are well known (Montgomery et al. 1996, Stewart et al. 2009, Cadol and Wohl 2010). Less studied is how LWD indirectly affects the spatial distribution of trophic interactions in freshwater ecosystems. In both the river and lake systems, models in which LWD interacted with fish to shape community structure performed better than models in which fish and LWD impacted the community independently. In both habitats, path coefficients leading from the Fish × LWD term to AFDM and to invertebrate densities were strongly negative, indicating that the presence of fish reduced these variables and that this fish effect was magnified in the presence of LWD. This pattern is consistent with strong fish consumption of AFDM and invertebrates and that LWD enhanced this consumption. The topological similarity in both river and lake path models provides robust evidence for the role of LWD piles in modulating fish control over benthic resources and indicates that interactions are better described as functions catalyzed by different physical and biological attributes rather than as constants.

There are two potential, but not mutually exclusive, mechanisms underlying the patterns involving the fish–wood aggregate variable in our study. First, the increased habitat complexity offered by the physical attributes of LWD may positively influence all trophic levels by creating refuge, altering flow patterns and providing stable substrate on which to settle. Given the lack of structural complexity outside LWD piles, small fishes may be especially attracted to these microhabitats because of the protection conferred from predators. For primary producers and heterotrophic microorganisms, LWD piles should provide a better habitat alternative to the otherwise unstable sandy substrate that dominates this Amazonian riverscape. Additionally, the role of LWD in retaining sediment and organic matter is

Fig. 3. Path diagrams depicting the two best-fit models in the lake. Details are the same as in Fig. 2. (A) Lake hypothesis 1 (LH1); (B) lake hypothesis 2 (LH2).
well established (Wallace et al. 2015). The second potential mechanism involves the food web role of LWD as an energy and nutrient subsidy to lower trophic levels. The positive impact of this energy pulse is well documented for invertebrates (Eggert and Wallace 2007, Wallace et al. 2015), algae, and heterotrophic microbes (Benke et al. 1984, Hoellein et al. 2010). Multiple authors have suggested that these energetic effects could percolate up the food web, ultimately providing an additional attractant to grazing, insectivorous, and omnivorous fish (Schindler et al. 2000, Wright and Flecker 2004), although experimental evidence is rare.

Disentangling between these potential mechanisms is challenging, but a key result derived from our experimental design and subsequent path analysis indicates that the first mechanism is likely responsible, at least over the short timescale evaluated. The best-fit path model did not include an independent effect of LWD on AFDM or invertebrates in the river. Although enhancing physical habitat alone has little effect on invertebrate production (Palmer et al. 2010, Wallace et al. 2015), if LWD had a direct trophic role, the nutrient and energy pulse offered by LWD should have increased AFDM and invertebrates on caged substrates in LWD treatments, a response that would have been detected as a direct positive path between LWD and response variables in the analysis. Because the experimental sampling substrates themselves provided solid substrate, the effects of having more available substrate would not have detectable effects on the experimental results (unless there is spillover, which is plausible for invertebrates, but not periphyton). Despite this evidence, the potential for other mechanisms may also be in place; however, the significant strong negative correlation between the aggregate variable and AFDM, and invertebrates, indicated that the results obtained were best explained by the association of fishes with LWD piles rather than an increased energy pulse affecting lower trophic levels.

A surprising result from this study stands in contrast with previous findings in similar Neotropical river basins (i.e., the Orinoco); we found no large fish exclusion treatment effect in the river. Previous studies have documented a strong influence of large grazing fishes on algal standing crops and AFDM accumulation, effects which cascade up the food chain to influence invertebrates (Flecker 1996, Hall et al. 2011). Although there are no comparable studies in Amazonia, the Orinoco’s food web structure is highly diverse and functionally similar (Albert and Reis 2011), and these fish-mediated effects are primarily due to the seasonal variation in flannel-mouthed characins (Prochilodontidae; Flecker 1996, Winemiller et al. 2014), which were typically observed in both the Manu River and the Cocha Cashu lake at the time of this study. However, being migratory and susceptible to overexploitation, interannual variation in the abundance of prochilodontids is common in the Manu River as in other river basins and their effects are not always discernable (J. Terborgh, personal communication).

Another important group of grazing fishes that similarly impact basal resources are armored catfish (Loricariidae), which we regularly caught when fishing with a gill net, although they were larger in the lake than in the river. In smaller Panamanian streams, Power (1990) found that potential predation of piscivorous birds concentrated on armored catfish, and their grazing effects on basal resources, in deeper waters. Although in the Manu River and lake, piscivorous birds regularly perch from LWD, they were rarely observed in our experimental treatments, which were conducted in shallow waters near the shoreline. Thus, potentially, large grazing fishes might impact basal resources in deeper areas of the river, while predation risks for smaller fishes by other fish trump risks associated with piscivorous birds. In summary, multiple factors might have led to a lack of a discernable effect of the large fish exclusion in the river, including not being in high enough abundances to have an effect, being dissuaded from feeding in our experimental treatments, or being constrained to other parts of the river. Lastly, although our treatments were large, they are dwarfed in comparison with the size of naturally occurring woodpiles in the river, and there might be a LWD pile size threshold for larger grazing fish such as prochilodontids as well as for fear-induced effects of piscivorous birds.

In contrast to the lack of effect of large grazers in the river, given the strong paths between the aggregate variable and AFDM, as well as invertebrates, LWD was likely most important for smaller omnivorous fishes, which were commonly observed feeding in LWD treatments. Similar
responses of AFDM and invertebrates to fish exclusions are well substantiated in other Neotropical streams where omnivorous fishes were strong interactors (Pringle and Hamazaki 1998), as well as in models (J. T. Wootton and C. M. Pringle, unpublished data). In the lake, on the other hand, the contribution of fishes cannot be prescribed with certainty since the path analysis revealed two alternative models that are statistically similar. The best-supported model (Lake H1; Fig. 3A) had a similar topology to that from the river in which the fish–wood aggregate variable negatively affected both AFDM and invertebrate densities. While this suggests LWD’s importance for omnivorous fishes, model Lake H2 (ΔAIC = 0.825; Fig. 3B) included a direct positive path between AFDM and invertebrates, but no effect of the aggregate variable. This model is congruent with the expectations that bottom-up mechanisms (e.g., resource availability) are structuring invertebrate densities. In this scenario, grazing fishes decreased detritus accumulation on hard surfaces, an effect subsequently cascading up the food web to decrease invertebrate densities (Flecker 1996, Hall et al. 2011, Winemiller et al. 2014). Without better probing the fish community composition, we will not be able to ascertain the ultimate drivers of these patterns. However, considered in combination with previous work, these results suggest that, in the river, benthic resources are affected by a diverse assemblage of smaller insectivorous, grazing, and/or omnivorous fishes, while size differences and trophic identity are indistinguishable in the lake.

Amazonian whitewater rivers that originate in the Andes tend to be rich in organic sediment of terrestrial origin, and a growing body of work suggests that secondary consumers in these systems are more likely to derive carbon from allochthonous detritus accumulating on the benthos rather than aquatic primary producers (Wissmar et al. 1981, Roach et al. 2014). Although chlorophyll a concentrations were generally low, they were strongly negatively correlated with experimental substrate depth (i.e., increasing distance from the surface). Rather than being controlled by animals or sedimentation, benthic primary productivity was primarily limited by turbidity, as expected in a large white water river with high sediment load. In contrast to the river, floodplain lakes typically have high water column primary productivity (Mortillaro et al. 2012), which may limit benthic productivity but also be the ultimate source of benthic AFDM accumulation (Cotner et al. 2006, Mortillaro et al. 2011). Isotopic studies from the Orinoco and other Amazon floodplain lakes support the notion that phytoplankton is an important contributor to benthic consumer energy budgets (Forsberg et al. 1993, Roach et al. 2009). Thus, in the lake, benthic energy budgets should be linked with littoral productivity, while in the river, benthic energy should be linked to allochthonous detrital resources, perhaps supplemented where LWD brings hard substrate for periphyton attachment nearer to the surface. Additionally, based on the evidence from installing substrates at varying depths, in the river and lake, LWD could facilitate primary production by decreasing light limitation, although the experiment was not designed to probe this. Lastly, in both ecosystems, benthic feeding is a widespread strategy and fishes might depend on hard surfaces, such as wood, to access these resources.

**Spanish cedar as a process catalyst**

Although Spanish cedar did not have a strong direct impact on basal resources, as LWD, it shifted the rates of interactions in both the river and lake. Suggesting this indirect role for LWD raises a general issue. Particularly, under what circumstances is it appropriate to prescribe strong interactor status to certain biological entities? Are there discernable functional characteristics that merit categorization as a keystone, engineering, or foundation species? Additionally, are these concepts appropriate for groups of species that play similar functional roles, rather than single dominant species? What if these functions change because of ecosystem context, or over a species ontogeny? Empirical and theoretical developments since Paine’s seminal work (1966, 1969) have provided compelling evidence that indirect interactions have a significant role in structuring ecosystems, and some biotic entities can be more important than others in influencing the distribution of these interactions across ecological networks (strong interactors; sensu Paine 1992). Concepts such as keystones species, ecosystem engineers, and foundation species have become important organizing principles guiding in ecology and conservation. However, because of their conceptual overlap and liberal use, this
terminology has been subject to considerable controversy. While several authors have focused on distinguishing details between concepts to clarify their applicability, pigeonholing a species into a particular category remains strongly subjective (Power et al. 1996, Wright and Jones 2006, Angelini et al. 2011).

Problematically, fitting species into a single definition is not straightforward because species can interact with communities through a variety of trophic and non-trophic pathways. Particularly important is parsing out the relative roles of modifying physical habitat and trophic interactions, because the structural effects often occur in conjunction with an increase in basal productivity and the modification of trophic interactions between community members. Disentangling structural and trophic factors is complicated because of the potential for feedback loops between these interacting axes and the difficulty to prescribe cause and effect. Our study was designed to probe a specific aspect of how Spanish cedar, as LWD, affects food webs, which, in combination with the common and well-documented notions about LWD, adds to the list of mechanisms by which riparian trees influence freshwater ecosystems. This influence goes beyond the clear roles that riparian trees have as suppliers and mediators of energy supply through input of leaves and removal of light in freshwater systems, and their role in shaping geomorphology. As with a variety of biotic entities, such as coral reefs (Shinzato et al. 2011, Foster et al. 2012) and whales (Roman et al. 2014), LWD could be described as keystone, foundation, and engineering species throughout different points in their ontogeny. However, doing so would partially overlook the totality of their multiple physical and trophic effects over the structure and function of communities and ecosystems. Thus, considering a holistic framework that integrates the physical, trophic, and energetic roles of strong interactors might be more appropriate for organisms such as LWD.

Keystones, ecosystem engineers, and foundation species share the common feature that they catalyze ecological processes that shape ecological communities in important ways. Processes can be as disparate as changing how carbon and nutrients are captured and flow through food webs (e.g., trophic cascades; Terborgh and Estes 2010), creating hotspots of high productivity via nutrient recycling and spatial concentration (Vanni 2002), altering soil formation and stability (Crowther et al. 2013), changing physical conditions (Wright et al. 2006, White and O’Donnell 2010), modifying species interactions, or a combination of these mechanisms. By altering process rates, these biological entities simultaneously influence multiple trophic levels through direct and indirect interactions at varying spatial and temporal scales, depending on their mobility, size, and distribution across the landscape. Ultimately, these process catalysters alter the rates of ecological mechanisms that influence the spatial distribution of interactions and thus the abundance and diversity of organisms across landscapes. Additionally, extirpation of these species can cause a considerable number of secondary extinctions, leading to substantial changes in community structure and ecosystem dynamics (Christianou and Ebenman 2005).

Previous efforts have concentrated on clarifying these concepts independently, leading to broad definitions, which often overlap. In contrast, recognizing their shared characteristics allows us to advocate for a narrower mechanistic view of keystones, ecosystem engineers, and foundation species that focuses on the process underlying how each group of species yields their influence over communities (Fig. 4); namely, this framework emphasizes that keystone species affect communities by directly changing the mode of trophic interactions, foundation species channel productivity into the creation of biomass, which forms the base on which the rest of the community resides, and ecosystem engineers modify physical context and stress through behavior. Thus, addition to or removal of a keystone, foundation species of engineer in a community would directly shift that community along one of those axes (e.g., trophic interactions, productivity, physical context), with the potential for cascades resulting from their indirect impacts. In contrast, addition or removal of a process catalyster would directly alter multiple processes simultaneously (i.e., interaction, productivity, physical stress). This process catalyster concept integrates the original conceptual definitions (e.g., keystones, Paine 1969, foundation species, Dayton 1972; ecosystem engineers, Jones et al. 1994), and emphasizes similarities among strong
interactors, while recognizing that these species can directly affect communities through a myriad of simultaneous mechanisms.

The keystone, ecosystem engineer, and foundation species concepts have been used to structure and inform ecosystem-based conservation efforts and have become common in ecological research and popular thought (Caro 2011). While the metaphors may capture key aspects of the complexity of ecological systems, without a guiding framework, their blurry and inconsistent use will continue to hamper communication of public science and improvement of conservation literacy (Barua 2011). In this study, path analysis of the river experiment and lake survey revealed that LWD interacts with fishes to influence basal resources in different ecosystem contexts. In combination with previous findings on LWD, these results suggest that LWD plays multiple trophic and non-trophic roles in freshwater ecosystems. However, considering LWD more holistically eludes traditional keystone, ecosystem engineers, and foundation species classification schemes. This intractability arises because, although the physical structure of a habitat strongly influences an ecosystem’s productivity and biodiversity (MacArthur and MacArthur 1961), the mechanisms by which physical structure itself is the determinant can be ambiguous. Consequently, as illustrated by other several groups of species (e.g., corals, mussels), existing concepts have been difficult to apply because of confusing terminology and the lack of an overarching classification framework. Understanding species through the processes they catalyze offers a framework that can be used to group keystones, ecosystem engineers, and foundation species along three independent axes, and aid in linking single species and ecosystem-based conservation strategies. Within the context of deforestation in the Amazon, considering LWD as a process catalyzer yields insights into how land-use change is influencing freshwater ecosystems and provides a more integrated target for conserving them.

ACKNOWLEDGMENTS

We are grateful to the Peruvian Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP), who granted us permission to conduct research in Manu National Park, the staff at the Cocha Cashu Biological Station for facilitating the research, and Hernán Ortega and Max Hidalgo from the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos for helping obtain permits. For help in the field, we thank Reynaldo Laureano, Fortunato Jaime Rayan, and Líveth Valenzuela Mendoza. Funding was provided by a National Geographic Young Explorer’s Grant (SAH), University of Chicago’s Center for Latin American Studies (SAH), and DOE Graduate Assistance in Areas of National Need Fellowship (SAH). Comments from Shahid Naeem improved the manuscript.

LITERATURE CITED

Albert, J. S., and R. E. Reis, editors. 2011. Historical biogeography of Neotropical freshwater fishes. University of California Press, Oakland, California, USA.
Allgeier, J. A., L. A. Yeager, and C. A. Layman. 2013. Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. Ecology 94:521–529.
Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean
coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society B 276:3019–3025.

American Public Health Association (APHA). 1998. Standard methods for the examination of water and wastewater. Twentieth edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Washington, D.C., USA.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity and conservation. BioScience 61:782–789.

Barua, M. 2011. Mobilizing metaphors: the popular use of keystone, flagship and umbrella species concepts. Biodiversity and Conservation 20:1427–1440.

Belcon, A. U. 2012. A limnological examination of the southwestern Amazon, Madre de Dios, Peru. Thesis. Duke University, Raleigh, North Carolina, USA.

Benke, A., C. T. Vanarsdall, D. M. Gillespie, and F. K. Parrish. 1984. Invertebrate productivity in a sub-tropical blackwater river—the importance of habitat and life-history. Ecological Monographs 54:25–63.

Bojesen, B. H., and R. Barriga. 2002. Effects of deforestation on fish community structure in Ecuadorian Amazon streams. Freshwater Biology 47:2246–2260.

Cadol, D., and E. Wohl. 2010. Wood retention and transport in tropical, headwater streams, La Selva Biological Station, Costa Rica. Geomorphology 123:61–73.

Caro, T. 2011. Conservation by proxy: indicator, umbrella, flagship, and other surrogate species. Island Press, Washington, D.C., USA.

Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumstead, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. North American Journal of Fisheries Management 4:947–963.

Christianou, M., and B. Ebenman. 2005. Keystone species and vulnerable species in ecological communities: Strong or weak interactors? Journal of Theoretical Biology 235:95–103.

Cotner, J. B., J. V. Montoya, D. L. Roelke, and K. O. Winemiller. 2006. Seasonally variable riverine production in the Venezuelan llanos. Journal of the North American Benthological Society 25:171–184.

Crowther, T. W., D. W. G. Stanton, S. M. Thomas, A. D. A’Bear, J. Hiscox, T. H. Jones, J. Votíšková, P. Baldrian, and L. Boddy. 2013. Top-down control of soil fungal community composition by a globally distributed keystone consumer. Ecology 94:2518–2528.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. Pages 81–96 in B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas, USA.

Eggert, S. L., and J. B. Wallace. 2007. Wood biofilm as a food resource for stream detritivores. Limnology and Oceanography 52:1239–1245.

Elton, C. 1927. Animal ecology. Reprinted 2001, University of Chicago Press, Chicago, Illinois, USA.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

Flecker, A. S. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–1854.

Forsberg, B. R., C. A. R. M. Araujo-Lima, L. A. Martinelli, R. L. Victoria, and J. A. Bonassi. 1993. Autotrophic carbon sources for fish of the central Amazon. Ecology 74:643–652.

Foster, N. L., I. B. Baums, J. A. Sanchez, C. B. Paris, I. Chollett, C. L. Agudelo, M. J. A. Vermeij, and P. J. Mumbly. 2012. Hurricane-driven patterns of clonality in an ecosystem engineer: the Caribbean coral Montastraea annularis. PLoS ONE 8:e53283.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.

Hall Jr., R. O., B. W. Taylor, and A. S. Flecker. 2011. Detritivorous fish indirectly reduce insect secondary production in a tropical river. Ecosphere 2:135.

Hoellien, T. J., J. L. Tank, J. J. Kelly, and E. J. Rosi-Marshall. 2010. Seasonal variation in nutrient limitation of microbial biofilms colonizing organic and inorganic substrata. Hydrobiologia 649:331–345.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Langford, T. E. L., J. Langford, and S. J. Hawkins. 2012. Conflicting effects of woody debris on stream fish populations: implications for management. Freshwater Biology 57:1096–1111.

MacArthur, R., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. M. Hood, B. W. Taylor, and S. A. Thomas. 2008. Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? Ecology 89:2335–2346.

Merritt, R. W., and K. W. Cummins. editors. 1996. An introduction to the aquatic insects of North America. Third edition. Kendall/Hunt Publishing Company, Dubuque, Iowa, USA.
Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools: an asset to corals. Science 220:1047–1049.

Montgomery, D. R., T. B. Abbe, J. M. Buffington, N. P. Peterson, K. M. Schmidt, and J. D. Stock. 1996. Distribution of bedrock and alluvial channels in forested mountain drainage basins. Nature 381:587–589.

Mortillaro, J. M., G. Abril, P. Moreira-Turcq, R. L. Sobrinho, M. Perez, and T. Meziane. 2011. Fatty acid and stable isotope (δ13C, δ15N) signatures of particulate organic matter in the lower Amazon River: seasonal contrasts and connectivity between floodplain lakes and the mainstem. Organic Geochemistry 42:1159–1168.

Mortillaro, J. M., F. Rigal, H. Rybarczyk, M. Bernardes, G. Abril, and T. Meziane. 2012. Particulate organic matter distribution along the lower Amazon River: addressing aquatic ecology concepts using fatty acids. PLoS ONE 7:e46141.

Ortega, H. 1996. Ictiofauna del Parque Nacional Manu, Madre de Dios, Peru. Pages 453–482 in D. Wilson and A. Sandoval, editors. Manu: the biodiversity of southern eastern Peru. Smithsonian Institution, Washington, D.C., USA.

Ortega, H., M. Hidalgo, G. Trevejo, E. Correa, A. M. Cortijo, V. Meza, and J. Espino. 2012. Lista anotada de los peces de aguas continentales del Perú: Estado actual del conocimiento, distribución, usos y aspectos de conservación. Ministerio del Ambiente, Dirección General de Diversidad Biológica – Museo de Historia Natural, UNMSM, Lima, Peru.

Osorio, D., J. Terborgh, A. Alvarez, H. Ortega, R. Quispe, V. Chipollini, and L. C. Davenport. 2011. Lateral migration of fish between an oxbow lake and an Amazonian headwater river. Ecology of Freshwater Fish 20:619–627.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91–93.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355:73–75.

Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? Freshwater Biology 55:205–222.

Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology 78:1146–1156.

Pettit, N. E., D. M. Warfe, M. J. Kennard, B. J. Pusey, P. M. Davies, and M. M. Douglas. 2013. Dynamics of in-stream wood and its importance as fish habitat in a large tropical floodplain river. River Research and Applications 29:864–875.

Power, M. E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. Ecology 71:897–904.

Power, M. E., D. Tillman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Dailey, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609–620.

Pringle, C. M., and T. Hamazaki. 1998. The role of omnivory in a Neotropical stream: separating diurnal and nocturnal effects. Ecology 79:269–280.

Pyron, M., A. P. Covich, and R. W. Black. 1999. On the relative importance of pool morphology and woody debris distributions of shrimp in a Puerto Rican headwater stream. Hydrobiologia 405:207–215.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roach, K. A., K. O. Winemiller, and S. E. Davis III. 2014. Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity and nutrients. Freshwater Biology 59:1278–1293.

Roach, K. A., K. O. Winemiller, C. A. Layman, and S. C. Zeug. 2009. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: evidence from stable isotopes. Acta Oecologica 35:513–522.

Roman, J. J. A. Estes, L. Morissette, C. Smith, D. Costa, J. McCarthy, J. B. Nation, S. Nicol, A. Pershing, and V. Smetacek. 2014. Whales as marine ecosystem engineers. Frontiers in Ecology and the Environment 12:377–385.

Ron, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in Western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Science 58:282–292.

Schindler, D. E., S. I. Geib, and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems 3:229–237.

Shinzato, C., et al. 2011. Using the Acropora digitifera genome to understand coral responses to environmental change. Nature 476:320–323.

Stewart, G. B., H. R. Bayliss, D. A. Showler, W. J. Sutherland, and A. S. Pullin. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecological Applications 19:931–941.

Taylor, B. W., A. S. Flecker, and R. O. Hall. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313:833–836.
Terborgh, J., and J. A. Estes, editors. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C., USA.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5:241–245.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. Ecology 96:1213–1228.

White, J. S. S., and J. L. O’Donnell. 2010. Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. Ecology 91:3538–3548.

Willis, S. C., K. O. Winemiller, and H. Lopez-Fernandez. 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142:284–295.

Winemiller, K. O., C. G. Montaña, D. L. Roelke, J. B. Cotner, J. V. Montoya, L. Sanchez, M. M. Castillo, and C. A. Layman. 2014. Pulsing hydrology determines top-down control of basal resources in a tropical river-floodplain ecosystem. Ecological Monographs 84:621–635.

Wissmar, R. C., J. E. Richey, R. F. Stallard, and J. M. Edmond. 1981. Plankton metabolism and carbon processes in the Amazon River, its tributaries and floodplain waters, Peru-Brazil, May–June 1977. Ecology 62:1622–1633.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community – interaction chains and interaction modifications. American Naturalist 141:71–89.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.

Wootton, J. T., and M. P. Oemke. 1992. Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. Environmental Biology of Fishes 35:311–319.

Wright, J. P., and A. S. Flecker. 2004. Deforesting the riverscape: the effects of wood on fish diversity in a Venezuelan piedmont stream. Biological Conservation 120:443–451.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.