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Biodiversity and ecosystem function in species-poor communities: community structure and leaf litter breakdown in a Pacific island stream

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Abstract. Pacific island stream communities are species-poor because of the effects of extreme geographic isolation on colonization rates of taxa common to continental regions. The effects of such low species richness on stream ecosystem function are not well understood. Here, we provide data on community structure and leaf litter breakdown rate in a virtually pristine stream on a remote island in the eastern Caroline Islands of Micronesia. The Yela River catchment on Kosrae, Federated States of Micronesia, is uninhabited, completely forested, and not traversed by any road. At each of 5 sampling stations along the Yela River we measured physical and chemical variables, characterized the benthic invertebrate community, and estimated the relative abundance of macroconsumers (fishes, shrimps, and snails) using snorkeling surveys and trapping. Benthic invertebrate biomass decreased with stream size and was dominated by macroconsumers (i.e., decapods and gastropods). Benthic insect species richness and density were extremely low, characterized by the complete absence of Ephemeroptera, Trichoptera, and Plecoptera, with nonshredding larval Chironomidae making up ~85% of the exceptionally low insect biomass (~0.6 mg dry mass/m^2). Six species each of fishes and shrimps and 4 snail species were found. We examined the functional role of these noninsect macroconsumers in organic matter processing by comparing litter breakdown rates inside and outside electrified macroconsumer-excluding quadrats at a single site in the lower Yela River. Breakdown rates were slow relative to those reported in most tropical litter decay studies ($k = 0.004$–0.018 among quadrats). Despite differences in macroconsumer density ($p = 0.01$), the leaf breakdown rate was not significantly different between reference and electrified treatments ($p = 0.77$). Thus, macroconsumers at this site had neither a direct role in shredding nor an indirect effect on leaf breakdown through their interactions with any nonexcluded taxa. In the absence of a significant role played by insect or macroconsumer shredders, leaf litter breakdown in streams of remote Pacific oceanic islands might be driven purely by physical and microbial processes. Our results suggest that biogeographic processes have placed some Pacific island streams at the extreme low end of a continuum of shredder biodiversity and biomass, restricting the ecosystem function of their species-poor communities.

Key words: biodiversity, biogeography, decay, decomposition, electric exclusion, insular, lotic, *Macrobrachium*, Pacific island, leaf-litter processing, tropical stream.

One approach to understanding relationships between ecosystem function and biodiversity is to study ecosystem processes in communities that have naturally low species richness. The Pacific Ocean, which covers ⅓ of the earth's surface and contains >10,000 islands, provides opportunities for study of many such communities. Pacific island systems often are isolated from neighboring islands and continental landmasses

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by hundreds of kilometers of open ocean. This isolation has resulted in unique and depauperate communities shaped by relative colonization ability and island age (Resh and de Szalay 1995, Craig 2003). In contrast to continental streams, aquatic insects are not major components of Pacific island stream communities, and insect assemblages are composed only of those species able to colonize over huge distances (Resh and de Szalay 1995). Instead, stream communities of the region typically are dominated by marine-derived diadromous taxa (i.e., fishes, shrimps, and snails; Resh et al. 1992, March et al. 2003a, Parham 2005). These differences in species richness and taxonomic community structure make Pacific island streams potentially valuable sites for comparative ecological studies, particularly those exploring relationships between biodiversity and ecosystem function.

One important role of stream consumers in determining ecosystem function is the processing of catchment-derived coarse particulate organic matter into smaller particles (i.e., shredding; Cummins 1973). In temperate stream ecosystems, shredding is carried out principally by insects (e.g., Trichoptera larvae and Plecoptera nymphs). Numerous studies have demonstrated the importance of insect consumers in the process of organic matter breakdown in temperate streams (e.g., Wallace et al. 1982). However, in tropical streams, particularly those on islands, shredding insects are often rare or absent (but see Cheshire et al. 2005, Yule et al. 2009), whereas other taxonomic groups (e.g., Crustacea) fill this functional role (Covich 1988, Wantzen and Wagner 2006). For example, few insect shredders are found in Puerto Rican streams, and the freshwater shrimp *Xiphocaris elongata* is the dominant shredder of leaf litter (March et al. 2001, Crowl et al. 2006).

Given the importance of such noninsect macroconsumers as shredders in many Caribbean island streams, it seems likely that noninsect shredders also might be found on Pacific islands. However, extreme geographic isolation and limited dispersal capabilities of many taxa could combine to filter out even shredding macroconsumer taxa from many island communities (Covich 2006). For example, *X. elongata* shares its habitat with several other shrimp species in Puerto Rican streams, but it is the only functional shredder among them (March et al. 2001). Thus, biogeographic processes on isolated Pacific islands might have resulted in communities with neither insect nor noninsect shredders and no role for nonmicrobial consumers in organic matter breakdown. Exploring this possibility requires information on community structure and the role of consumers in organic breakdown in Pacific streams. Unfortunately, Pacific island stream communities are poorly characterized, and litter processing studies from the Pacific region are even more rare (but see Larned 2000, Larned et al. 2003).

We had 2 primary objectives. First, we sought to characterize the community of a virtually pristine Pacific island stream in eastern Micronesia. Our goal in this longitudinal survey was not an exhaustive species list, but a description of the functional structure of a representative intact community that could be compared with those typical of continental streams and those of relatively well studied, but disturbed Pacific island systems (e.g., Hawaii; Brasher 2003). Second, we examined the consequences of extreme taxonomic simplicity on breakdown and use of terrestrial organic matter. Specifically, we asked the question: In the absence of insect shredders, have diadromous (noninsect) macroconsumer taxa filled this trophic niche, or can extreme biogeographic isolation leave some Pacific island stream communities essentially without functional shredders?

Methods

Study site

The island of Kosrae is in the eastern Caroline Islands in the equatorial western Pacific Ocean (lat 5°16′ to 5°22′N, long 162°54′ to 163°02′E; Fig. 1). Kosrae is the easternmost island-state in the Federated States of Micronesia. Kosrae is a small (112 km^2) volcanic high island (maximum elevation = 629 m) between 1.2 and 2.6 million years old (Keating et al. 1984). Annual mean temperature is 27°C, and average annual rainfall ranges from 5000 mm at the coast to 7500 mm in the interior (Whitesell et al. 1986). Marked seasonality in rainfall and temperature is not evident on Kosrae (Krauss et al. 2006). The island has 97% forest cover composed of natural forest, agroforest, and secondary formations (Whitesell et al. 1986).

The Yela River is a small (4th-order) stream that flows into the Pacific on Kosrae's western side (Fig. 1) through what might be the least disturbed catchment in Micronesia. The catchment vegetation consists of mangrove forest (dominated by *Sonneratia alba* and *Bruguiera gymnorrhiza*) at its estuary, mature freshwater swamp forest (dominated by *Terminalia carolinensis* and *Pandanus* spp.) up to 40 m asl, and undisturbed upland forest (dominated by *Campnosperma brevipetiolata*) above 40 m asl (Whitesell et al. 1986). The catchment is not inhabited, no roads enter it, and occasional hunting and scattered agroforestry are the only significant human activities.

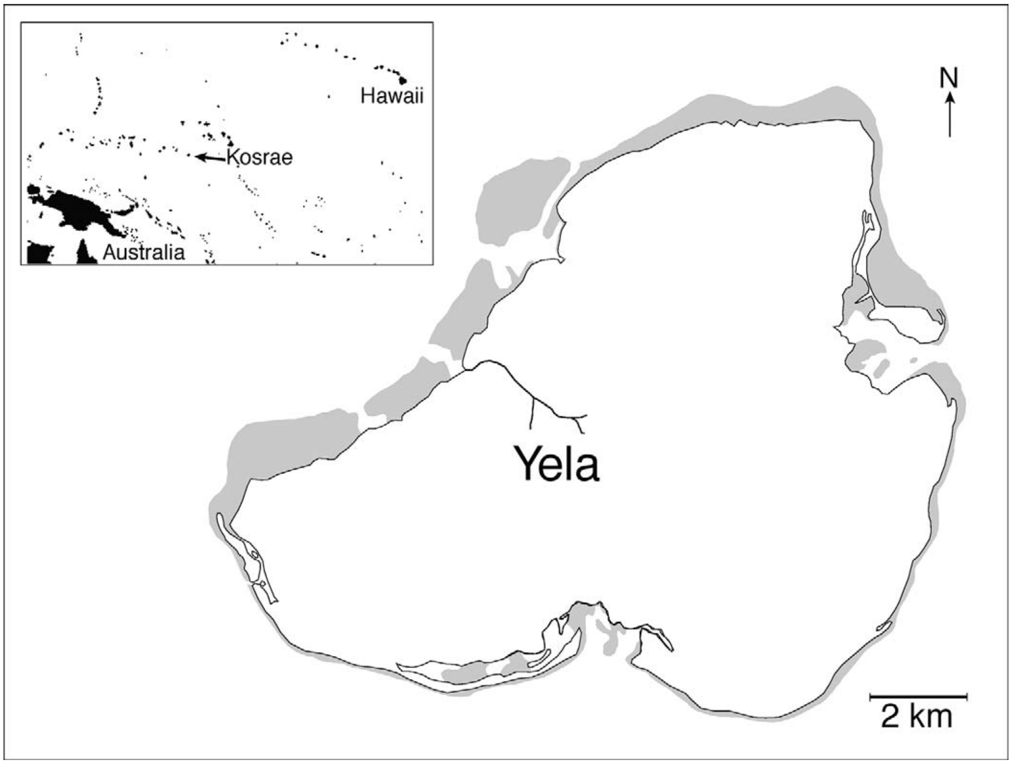

FIG. 1. The Yela River on Kosrae, Federated States of Micronesia. Inset shows the location of Kosrae in the Pacific Ocean.

Community structure

We conducted the survey on 27–28 November 2000. On 27 November, we established 5 sampling stations and took physical measurements that included: channel width, maximum channel depth, and % canopy cover at 10-m intervals along a representative 50-m reach, water temperature and conductivity, latitude/longitude coordinates and altitude (estimated using a hand-held global positioning system [Magellan Navigation, Inc., Santa Clara, California] and topographic map), and discharge. We measured % canopy cover with a spherical densitometer (Ben Meadows Company, Janesville, Wisconsin), and we measured water temperature and conductivity with a digital meter (Hanna Instruments, Woonsocket, Rhode Island). Before leaving each station, we left 1 baited minnow trap for shrimp sampling.

We sampled water for chemical variables and biota the following day. We collected replicate filtered (0.45-μm Millipore®; Millipore Corporation, Billerica, Massachusetts) water samples from each station for nutrient and dissolved organic C (DOC) analysis. We stored samples in a cooler and froze them within 12 h. We measured water temperature and conductivity again at each station as described above. At each station, we took 5 Surber samples from areas with representative substratum and water velocity. We also collected 5 leaf pack grabs. We preserved all benthic samples immediately in 70% ethanol. To document the presence of macroconsumer taxa, we collected the contents of the baited traps and searched for individuals of additional taxa. To quantify the abundance of macroconsumers, we conducted timed (1-min) snorkeling surveys in each of the five 10-m sections at each sampling station. Snorkelers examined the entire streambed in each section and counted fishes (gobiids, *Anguilla marmorata*, and *Kuhlia* spp.), atyid shrimps, *Macrobrachium* spp., and gastropods. Fishes also were collected by angling (*Kuhlia* spp.), by hand (*A. marmorata*), and by snorkelers who corralled individuals (i.e., small gobiids) into Surber samplers.

We transported water samples to the University of Georgia, where we analyzed them for NO_3+NO_2-N (Cd reduction method), NH_4-N (phenate method), and soluble reactive P (ascorbic acid method) with an Alpkem RFA 300 automated analyzer (OI Analytical, College Station, Texas) (APHA 1985). We analyzed samples for DOC on a Shimadzu TOC-5000A total organic C analyzer (Shimadzu Corporation, Columbia, Maryland).

We removed leaf litter from leaf pack samples within 24 h of sampling, dried it for 3 d at 60°C, and cooled and weighed it. We combusted a representative, weighed subsample at 500°C for 2 h, and cooled and reweighed it for determination of leaf-pack ash-free dry mass (AFDM). We transported entire benthic and leaf pack samples to the University of Georgia, where we stained them with rose Bengal dye and removed all macroinvertebrates. We measured lengths (longest axis) of nondecapod invertebrates to the nearest 0.5 mm under a stereomicroscope fitted with an eyepiece micrometer. We measured postorbital carapace lengths of shrimps and carapace widths of crabs. We calculated biomass using length–mass regressions for invertebrates in the same genus, family, or order (Luppi et al. 1997, Benke et al. 1999, Greathouse 2005, A. D. Huryn, University of Alabama, unpublished data, W. F. Cross, Montana State University, unpublished data). We expressed benthic and leaf pack invertebrate biomass data as mg dry mass [DM]/m^2 and mg DM/g AFDM leaf litter, respectively.

We expressed snorkeling observation data as mean numbers of gobiids, *Kuhlia* spp., *A. marmorata*, atyids, *Macrobrachium* spp., and gastropods observed per minute. We identified freshwater shrimps with keys in Chace (1983) and unpublished material (JWS, unpublished data). Fishes were identified by Lynne Parenti (Smithsonian Institution, Washington, DC). Snails were identified by Alison Haynes (University of the South Pacific, Fiji).

Litter breakdown

We conducted a leaf litter breakdown experiment in which the presence and absence of macroconsumer taxa was manipulated with electric exclosures from 17 October to 25 November 2000. For logistical reasons (i.e., no trail system existed in the Yela catchment), we conducted the experiment in the lower Yela River at 3 m asl (~150 m downstream from station 1). We established a 100-m reach, along which we placed 5 pairs of experimental quadrats near the banks of the river. We anchored quadrats to the stream bottom with plastic cable ties and large cobbles and positioned them ≥0.5 m apart. Quadrats were square frames (50 × 50 cm) made of 19-mm chlorinated polyvinyl chloride (CPVC) tubing, with an inner and outer square of uninsulated 12-gauge Cu wire held to the CPVC frame with plastic cable ties. We flipped a coin to determine which frame would be electrified (macroconsumer exclusion) or be a control (macroconsumer access). We used the electric exclosure technique first described by Pringle and Blake (1994) and later modified by Pringle and Hamazaki (1997). Each macroconsumer exclusion quadrat was connected to a 12-V solar-powered fence charger (Parker–McCrory Manufacturing Company, Kansas City, Missouri). The electricity excluded large fishes and shrimps (>2.5 cm) but not insects, juvenile shrimps, and other small invertebrates. We changed batteries every 5 d to maintain a strong charge. We measured water depth and velocity in the middle of each quadrat on 3 dates to ensure that leaf packs of both treatments were experiencing similar physical conditions.

We tethered five 10-g packs of air-dried leaves of the dominant swamp forest tree species, *T. carolinensis*, in each quadrat. On day 0, we sampled 24 leaf packs to obtain an air- to oven-dried conversion factor that we used to adjust the original air-dried masses of the leaf packs. We sampled 1 leaf pack randomly from each quadrat on days 3, 6, 13, 24, and 39. We collected leaf packs with a fine-mesh net, rinsed them with filtered water, dried them at 60°C for ≥48 h, and weighed them to the nearest 0.1 g. We calculated leaf decay rate (k) for each quadrat separately by regressing the natural log of % leaf mass remaining against elapsed days (k is the negative slope of the regression; Benfield 1996). We measured the ratio of total C to N (C:N) of 5 day-0 packs and every leaf pack sampled to examine changes in microbial colonization and leaf quality through time. Subsamples of leaf packs were ground into powder with a ball mill and analyzed with a Carlo Erba NA 1500 CHN analyzer (Carlo Erba Instrumentazione, Milan, Italy).

We preserved invertebrates found in each leaf pack in 70% ethanol and identified them to order or family. We made 2-min observations of each quadrat on 5 dates to identify macroconsumers (shrimps and fishes) in the quadrats and to quantify the effectiveness of the electrical exclusion technique. We conducted observations during the day on 3 dates and at night on 2 dates because shrimp and fish activity can vary between night and day (Johnson and Covich 2000). We counted all shrimps and fishes observed within the quadrat (i.e., not necessarily on the leaf packs).

We sampled chironomids and *Macrobrachium lar* (the only common benthic taxa at this site) for stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) and gut content analysis to examine the relative importance of leaf litter to the food web at the lower Yela study site. We sampled a total of 5 individual chironomids and *M. lar* for gut content analyses. We removed guts from organisms under a dissecting microscope, suspended them in water, and filtered them onto 25-mm membrane filters (Metricel GN-6 gridded, 0.45-μm pore size; Gelman Sciences Inc., Ann Arbor, Michigan). We dried filters for 20 min at 40°C, placed them on slides, and cleared them with immersion oil. We placed cover slips onto the filter and sealed them with clear nail varnish. We categorized gut contents as amorphous detritus, leaf and wood detritus, diatoms, filamentous algae, and animal material. We sampled 3

TABLE 1. Physical and chemical characteristics of the 5 sites sampled on the Yela River, Kosrae, Federated States of Micronesia, 27 to 28 November 2000. $n = 2$ for each chemical variable; temperature and conductivity were measured on both 27 and 28 November 2000. BD = below detection limits.

	Station				
Variable	1	2	3	4	5
Elevation (m asl)	3	3	66	100	150
Mean channel width (m)	10.9	7.0	5.2	2.8	2.4
Mean maximum depth (m)	0.5	0.4	0.4	0.2	0.1
Discharge (L/s)	690	470	140	50	30
Mean canopy cover (%)	98	98	99	97	98
NO_3+NO_2-N (μg/L)	10	BD	BD	16	8
NH_4-N (μg/L)	BD	BD	BD	BD	BD
Soluble reactive P (μg/L)	61	63	66	101	76
Dissolved organic C (μg/L)	626	506	521	753	574
Temperature (°C)	26.6	25.7	25.6	25.1	24.9
Conductivity (μS/cm)	84.8	83.3	90.8	106.3	105.7

chironomids and 3 *M. lar* for isotope analysis. We combined chironomids to obtain sufficient mass for analysis. We analyzed muscle tissue from individual shrimps separately. We collected 3 replicates ($n = 3$) of coarse particulate organic matter (CPOM) from the stream bottom along the 100-m reach. We sampled periphyton ($n = 3$) by scraping stream cobble. We collected fine benthic organic matter (FBOM, $n = 1$) as a composite sample from the stream bottom and obtained seston ($n = 1$) by filtering 3 L of stream water through a glass-fiber filter (0.7-μm pore size). We dried all samples at 60°C for ≥48 h. We ground CPOM into powder with a ball mill. We combusted all samples to CO_2 and N_2 and analyzed in a Carlo Erba NA 1500 CHN analyzer connected to a Finnegan Delta C mass spectrometer. We calculated stable isotope signatures as:

$$\delta^{13}C \text{ or } \delta^{15}N(‰) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

where R is ($^{15}N/^{14}N$) or ($^{13}C/^{12}C$). Standards were PDB carbonate for C and atmospheric N_2 for N.

Statistical analyses

We compared macroconsumer abundance, leaf decay rate (k), water depth, and water velocity between treatments (macroconsumer access vs macroconsumer exclusion) with 1-way analyses of variance (ANOVAs). We used a repeated-measures ANOVA to test for differences in nonshrimp invertebrate abundance between treatments. We $\log_{10}(x)$-transformed abundance data to improve normality. We compared decay rate and nonshrimp invertebrate abundance with 4 replicate pairs on days 3 through 24 because of missing values (lost leaf packs). We did all statistical analyses with JMP 3.1.5 (SAS Institute, Cary, North Carolina).

Results

Physicochemical variables

Our sampling stations ranged from the 4th-order downstream station 1 at 3 m asl to the 2nd-order station 5 at ~150 m asl (Table 1). Along this continuum, baseflow discharge was 690 L/s at station 1 and 30 L/s at station 5, average channel width ranged between 10.9 and 2.4 m, and average maximum channel depth ranged between 0.5 and 0.1 m. Canopy cover was ≥97% at every sampling station.

Water temperature ranged between 26.6°C at the downstream station 1 and 24.9°C at the upstream station 5 (Table 1). Conductivity declined along the stream in a downstream direction (105.7–84.8 μS/cm). Concentrations of NO_3+NO_2-N and NH_4-N were extremely low at all sampling stations; NH_4-N was consistently below detection limits, whereas NO_3+NO_2-N ranged from concentrations below detection limits to 16 μg/L. Concentrations of soluble reactive P were relatively high and ranged between 61 and 101 μg/L. DOC concentrations were low to moderate (506–753 μg/L).

Benthic and leaf-pack grab samples

Total benthic invertebrate biomass generally increased with elevation, but variability among Surber samples and leaf-pack grabs was high (Fig. 2A, B). Decapods and gastropods constituted most of the benthic invertebrate biomass from both Surber samples and leaf litter, with other groups at extremely low

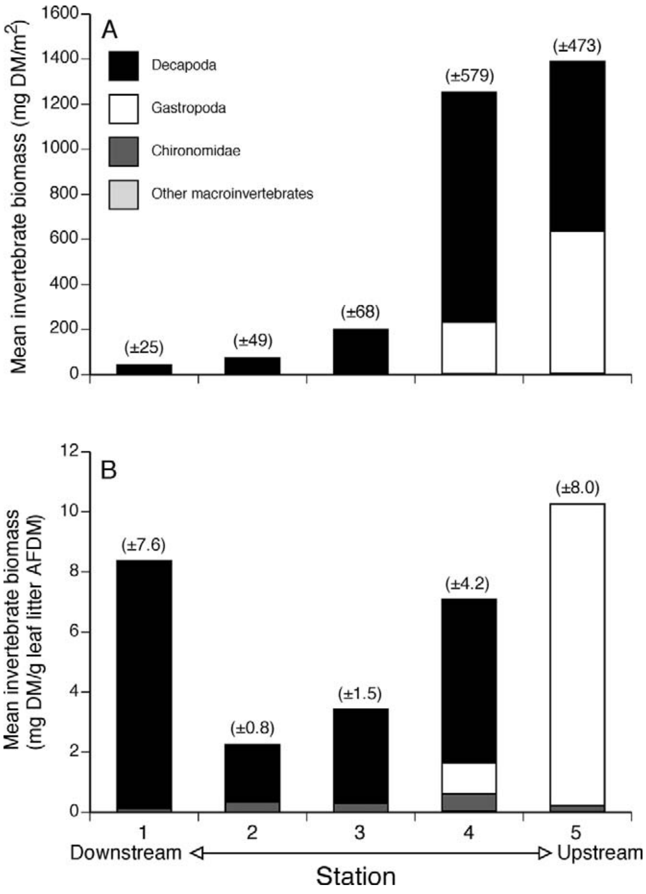

FIG. 2. Mean (±1 SE for total biomass) macroinvertebrate biomass in benthic samples (A) and leaf-litter grab samples (B) at 5 stations along the Yela River, Micronesia, in November 2000. Biomass of Chironomidae and other macroinvertebrates was often too low to represent. DM = dry mass, AFDM = ash-free dry mass.

densities (Fig. 2A, B). *Melanoides tuberculata* was the only gastropod found in Surber samples and leaf-pack grabs and was present only at stations 4 and 5. All decapods found in benthic samples were atyid shrimps, except 1 grapsid crab at the lowest station and 1 *Macrobrachium* shrimp at the highest station. Chironomids constituted most (~85%) of the insect biomass, which was exceptionally low (mean = 0.6 mg DM/m^2 in the benthic samples). We did not systematically identify chironomids beyond family, but we did record the genera *Chironomus* and *Tanytarsus* in the lower reaches of the Yela River as part of our study. Oligochaeta was the only other taxon frequently found. Very rare taxa included larval coenagrionid zygopterans (Odonata), pyralid moth larvae (Lepidoptera), tipulid larvae (Diptera), amphipods, and polychaetes.

TABLE 2. Fish, crustacean, and gastropod species sampled or observed at the 5 stations along the Yela River, Kosrae, Federated States of Micronesia, 27 to 28 November 2000.

	Station				
Species	1	2	3	4	5
Fishes					
Anguillidae					
Anguilla marmorata	X	X		X	X
Kuhliidae					
Kuhlia spp.[a]	X	X	X	X	X
Gobiidae					
Gobiinae					
Stenogobius genivittatus	X				
Redigobius bikolanus	X				
Sicydiinae					
Stiphodon sp.	X	X	X	X	
Decapoda					
Palaemonidae					
Macrobrachium lar	X	X	X	X	X
Macrobrachium latimanus				X	X
Atyidae					
Caridina typus		X	X		
Caridina weberi				X	
Atyopsis spinipes		X		X	
Atyoida pilipes				X	X
Gastropoda					
Neritina canalis				X	X
Neritina pulligera	X	X			
Clithon castanea		X			
Melanoides tuberculata					X

[a] *K. rupestris* and *K. marginata*

Snorkeling surveys and trapping

Several fish taxa were recorded at all, or most, of the sampling stations along the Yela River continuum. These included the giant mottled eel *Anguilla marmorata*, flagtails *Kuhlia* spp. (*Kuhlia rupestris* and *Kuhlia marginata* could not be distinguished), and the sycidiine gobiid *Stiphodon* sp. (Table 2). Two other gobiids were restricted to the lowermost station (Table 2). The 2 palaemonid shrimp taxa showed different distributions: *M. lar* was present at every station, whereas *Macrobrachium latimanus* was restricted to the 2 highest stations. The atyids *Caridina typus* and *Atyopsis spinipes* were only found at intermediate stations, whereas *Atyoida pilipes* appeared to be restricted to the 2 highest stations. *Caridina weberi* was only found at station 4 (Table 2). Gastropods in the Yela River also displayed marked elevational zonation and were present either at low stations (*Neritina pulligera* and *Clithon castanea*) or at high stations (*Neritina canalis* and *M. tuberculata*) (Table 2).

Snorkeling surveys provided additional data on relative abundances of macroconsumers at each sampling station (Fig. 3). Gobiid fishes were the most

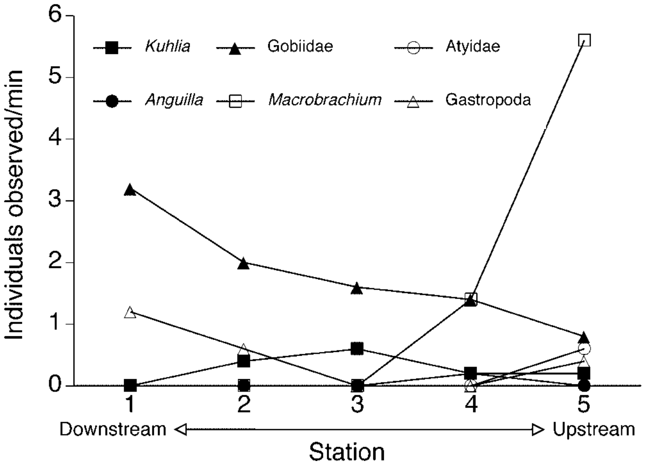

FIG. 3. Mean encounter frequency of major macroconsumer groups observed during timed snorkeling surveys at 5 stations along the Yela River, Micronesia, in November 2000.

common macroconsumers at stations 1 through 4, and relative abundances declined steadily upstream (Fig. 3). *Kuhlia* spp. were present at low densities at every sampling station (Fig. 3, Table 2), but were not always observed during snorkeling. The giant mottled eel was observed in low densities at all stations except Station 3. Atyid and palaemonid shrimps were present at all stations but more were observed at stations 4 and 5 than elsewhere (Fig. 3). On the basis of snorkeling observations, relative snail abundance was greatest at the low stations (1 and 2), 0 at the middle stations, and low at the highest stations (Fig. 3) and reflected the species distributions described above.

Litter breakdown rate

The electric exclusion experiment successfully reduced macroconsumer access to leaf packs. A few fishes and shrimps were able to enter electrified quadrats during periods of low battery charge, but the mean number of macroconsumers observed was significantly higher in the control (1.8 ± 0.54 SE, df = 49, $F = 7.09$, $p = 0.01$) than the electric exclosures (0.32 ± 0.15). Most (77%) of macroconsumers observed in control quadrats were shrimps. Shrimps were not identified to species during the observation period, but appeared to be mostly *M. lar.* The few fishes observed in the quadrats were small juveniles and usually were in the water column above the leaf packs. Mean water depth (control = 18.2 ± 1.0 cm, exclosure = 18.3 ± 2.3 cm) and mean water velocity (control = 0.07 ± 0.02 m/s, control = 0.08 ± 0.02 m/s) over the leaf packs did not differ between treatments (df = 29, $F = 0.002$, $p = 0.96$ and df = 29, $F = 0.27$, $p = 0.61$, respectively).

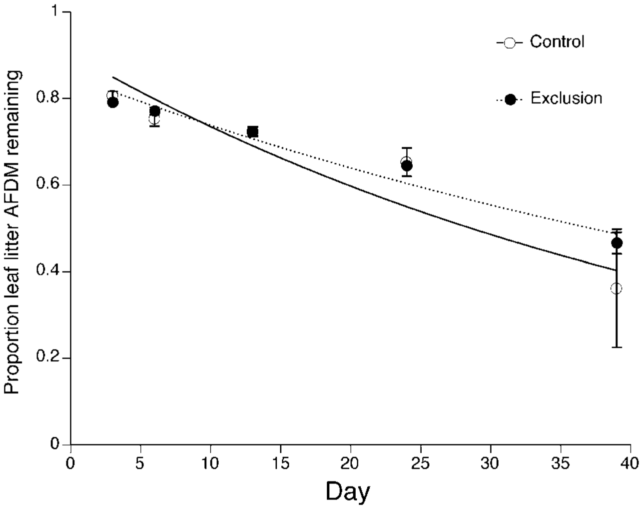

FIG. 4. Mean (±1 SE) proportion of ash-free dry mass (AFDM) leaf litter remaining in macroconsumer access (control) and electrified macroconsumer exclusion quadrats during the 39-d litter study on the lower Yela. Fitted curves are the exponential decay model.

Leaf decay rates (k) varied between 0.004 to 0.018 and did not differ significantly between macroconsumer access treatments (df = 7, $F = 0.10$, $p = 0.77$; Fig. 4). C:N ratio (an inverse index of litter quality) was similar between treatments and decreased steadily through time, a result that indicated similar rates of microbial colonization between macroconsumer access treatments (Fig. 5).

Macroconsumer access treatments differed with respect to the number of nonshrimp invertebrates (mostly chironomids and oligochaetes) that colonized leaf packs ($p = 0.02$; Fig. 6). Gut analyses revealed that

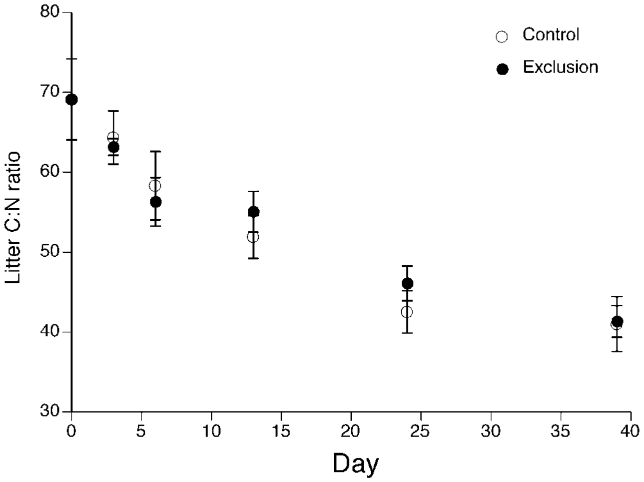

FIG. 5. Mean (±1 SE) C:N ratio of remaining leaf litter in macroconsumer access (control) and electrified macroconsumer exclusion quadrats during the 39-d litter study on the lower Yela. AFDM = ash-free dry mass.

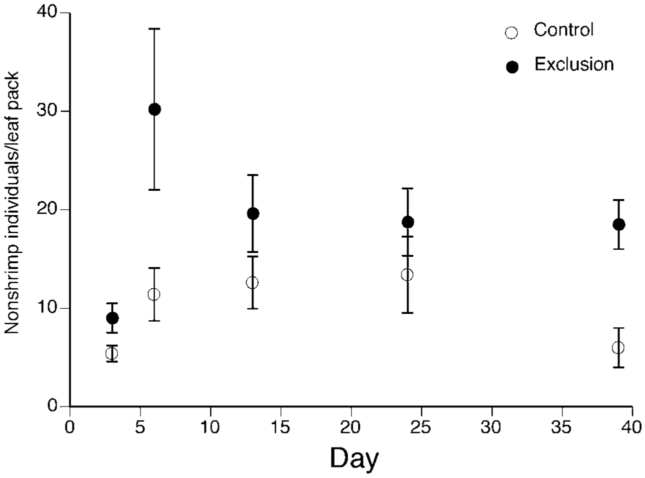

FIG. 6. Mean (±1 SE) abundance of nonshrimp invertebrates in leaf litter packs in macroconsumer access (control) and electrified macroconsumer exclusion quadrats over the 39-d litter study on the lower Yela.

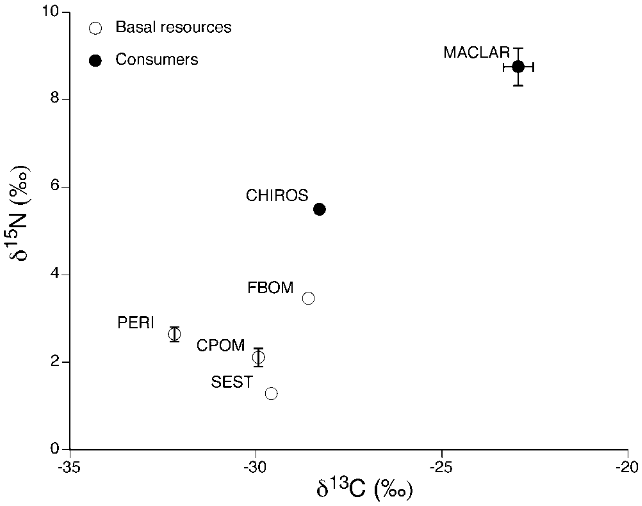

FIG. 7. Mean (±1 SE) stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of major basal resources and 2 numerically dominant invertebrate consumers in the lower Yela River. PERI = periphyton, CPOM = coarse particulate organic matter, SEST = seston, FBOM = fine particulate organic matter, CHIROS = chironomids, MACLAR = *Macrobrachium lar.* Values without error bars were based on a single measurement.

chironomids, the dominant nonshrimp invertebrate found in leaf packs, consumed mostly amorphous detritus (>85% of particle area) and no significant amounts of leaf litter (data not shown). Gut analyses of *M. lar*, the dominant shrimp at the site, also showed minimal consumption of leaf litter (data not shown). These patterns of consumption were supported by the stable isotope analysis. Based on $\delta^{13}C$ and $\delta^{15}N$ values, chironomids appeared to be more dependent on FPOM, which could have been derived from CPOM (Fig. 7). The $\delta^{13}C$ and $\delta^{15}N$ values of the shrimp *M. lar* indicated that it is a predator in this food web and unlikely to be an important shredder of leaf litter (Fig. 7).

Discussion

Community structure

Results from our longitudinal survey showed that the Yela stream macrofaunal community was much simpler than those of tropical continental streams (e.g., Cheshire et al. 2005) and those of other tropical island streams (e.g., Greathouse and Pringle 2006). Species richness was low, and the assemblage was taxonomically restricted. In particular, insects were present at extremely low species richness, abundance, and biomass. Mean insect biomass in benthic samples from our survey was >1000× lower than that typical of forest streams in the continental US (Huryn et al. 2008). No Ephemeroptera, Plecoptera, or Trichoptera were present, and only chironomids (Diptera) were found in any abundance (albeit at extremely low biomass relative to decapods and gastropods). Other insect taxa (e.g., tipulids, pyralids, and zygopterans) were found only very rarely. Undoubtedly, more freshwater insect taxa exist in the Yela River watershed and on Kosrae. However, our results underscore the extreme simplicity of stream insect communities on remote Pacific islands, driven by the limits of dispersal over great distances of open ocean. This simplicity presumably has left empty trophic and habitat niches that usually are occupied in more complex communities. For example, a recent extensive search for odonates (a relatively strong-flying group as adults) on Kosrae found that forest streams were largely unexploited or underutilized habitat (Buden and Paulson 2003). Many other insect groups do not appear to be play a significant role in the Yela River's benthic community.

In the absence of a diverse and abundant insect community, the stream fauna of the Yela River was dominated instead by a relatively simple community of diadromous macroconsumers, composed of 16 species of fishes, shrimps, and snails. Dominance by such marine-derived taxa is characteristic of insular streams globally (e.g., March et al. 2003b, Smith et al. 2003, Resh 2005). However, species richness of macroconsumer taxa in the Yela River was low relative to other tropical island stream communities (e.g., Puerto Rico; Covich and McDowell 1996). Moreover, many taxa in this group showed a high degree of zonation along the Yela River continuum. This zonation reduces site-specific species richness and highlights the importance of a longitudinal approach to characterizing the community of this relatively short river system.

Decapods were the most common macroconsumer and contributed most of the benthic invertebrate biomass at most stations. We found 6 species of shrimps: 2 palaemonids and 4 atyids, of which 1 palaemonid (*M. latimanus)* and 3 atyids (*C. typus*, *C. weberi*, and *A. spinipes*) have not been reported from Kosrae previously. We did not find one species of atyid (*Caridina serratirostris*) that has been reported from the Inem stream on the eastern side of Kosrae (March et al. 2003a). The palaemonids differed in their distribution. *Macrobrachium lar* was present at all 5 stations, whereas *M. latimanus* was restricted to the upper 2 high-elevation stations. Both species are found on Pohnpei where they have similar distributions to those observed on Kosrae, with a greater number of *M. latimanus* found in higher elevation headwater streams (Buden et al. 2001a). The atyid species also varied in their longitudinal distribution. Large *A. pilipes* were found only at the higher elevations (stations 4 and 5), where they were under cascading water on the sides of boulders and large cobble. A similar longitudinal distribution and microhabitat selection for *A. pilipes* was reported in Pohnpei (Buden et al. 2001a). *Caridina typus*, *C. weberi*, and *A. spinipes* were only found at mid-elevation sites (stations 2–4). These 3 taxa have a broad distribution throughout the Indo-West Pacific and occur on neighboring Pohnpei (Maciolek and Ford 1987, Buden et al. 2001a).

We found 4 species of snails. *Neritina pulligera*, *N. canalis*, and *M. tuberculata* are found throughout the Asia Pacific region, and *C. castanea* has been reported from the Caroline Islands, Samoa, and Fiji (A. Haynes, University of South Pacific, personal communication). Only *N. pulligera* has been previously reported on Kosrae (March et al. 2003a). Marked zonation in the distribution of snails with elevation or distance from the river mouth has been observed in other tropical island streams (e.g., Haynes 1985). We found *N. canalis* and *M. tuberculata* only at our 2 highest stations. This pattern was somewhat surprising because *M. tuberculata* is parthenogenetic, a habitat generalist, and often one of the most commonly found snails in tropical island streams (Haynes 1990, 2000). *Neritina canalis*, like other neritid snails, is thought to be amphidromous, with larval development occurring in marine environments (Tina Liu and Resh 1997, Resh 2005). We did not observe neritids actively migrating (e.g., Schneider and Frost 1986), but we might have missed smaller neritids at the lower elevations.

Five of the 6 fish species we found have been reported elsewhere on Kosrae (Donaldson and Myers 2002, March et al. 2003a) and also occur on Pohnpei (Maciolek and Ford 1987, Buden et al. 2001b). The fish assemblage of the Yela was typical of high island streams in that 3 of the 6 species were gobies. *Stenogobius gennivittatus* has not been reported previously from Kosrae or Pohnpei. However, this goby has a broad Indo-West Pacific distribution (e.g., Fiji; Ryan 1991). Additional fish taxa sampled in streams of Kosrae by the authors (JPB and JGM) include *Ophiocara porocephala*, *Stenogobius* sp., *Microphis brachyurus*, *Stiphodon pelewensis*, *Glossogobius celebius*, *Ophieleotris aporos*, *Caranx sexfasciatus* (juveniles), and *Lutjanus argentimaculatus* (juveniles). Several of these taxa are euryhaline and found in locations closer to the saltwater margin of the estuary than where we sampled (see Donaldson and Myers 2002 for a list of freshwater fishes found on Kosrae).

Litter breakdown

We found no treatment effect of macroconsumer access on leaf litter breakdown at our lower Yela River study site. This result suggests that the macroconsumer taxa present, and particularly the dominant shrimp *M. lar*, were not shredders. Higher numbers of nonshrimp invertebrates in macroconsumer exclusion quadrats indicated that macroconsumers had some direct (probably predatory) effect on nonshrimp invertebrates. However, significant increases in nonshrimp invertebrate abundance in the absence of macroconsumers, combined with no treatment difference in litter decay rates, suggests that the nonshrimp invertebrates that responded to low macroconsumer densities also were not shredders. The litter species we chose for the exclusion study could have been unpalatable to any shredders present at the lower Yela site. We lack leaf chemistry data for *T. carolinensis*, but breakdown rate of a species in the same genus (*Terminalia oblonga*) was 3.9%/d in a Costa Rican stream. This value was an intermediate rate among 8 species picked to represent a range in leaf chemistry (Ardón and Pringle 2008). Combined with the evidence for microbial colonization provided by changes in C:N ratio, these data suggest that the litter species we chose for the breakdown study would have been palatable to shredders had they been present.

Several additional lines of evidence point to a paucity or absence of shredder taxa in the Yela river system. With the exception of 3 small tipulid larvae, no representatives of insect groups usually associated with shredding (e.g., Trichoptera, Plecoptera) were found on Kosrae. The few other insect taxa found were either extremely rare representatives of other functional feeding groups (e.g., grazing pyralids) or were shown by gut analysis not to consume leaf litter directly (e.g., chironomids). Stable isotope analysis of potential basal resources and of 2 dominant consumers

(*M. lar* and chironomids) also indicated that consumption of leaf litter was unlikely, at least at the lower Yela site. Other macroconsumer taxa were either never observed in leaf packs (e.g., fishes) or unlikely to be shredders because of morphology (e.g., filter-feeding atyid shrimps, scraping snails). Last, we never saw any evidence of shredding activity on leaf material collected from leaf packs, and leaf decay rates in the quadrats were relatively slow (0.4–1.8%/d) for such high water temperatures (a relatively constant 26°C). The taxa present at sites upstream from our exclusion experiment could have constituted a functional shredder community, but we failed to find strong evidence for such a pattern in our survey. Various hypotheses have been put forward to explain scarcity or loss of insect shredders in most tropical streams (but see Cheshire et al. 2005) and their replacement by other taxonomic groups. These hypotheses include biogeographic processes (Covich 2006, Wantzen and Wagner 2006) and competitive interactions with heterotrophic microbes at relatively high water temperatures (Irons et al. 1994). Our community and litter breakdown data suggest that biogeographic processes play an overridingly important role in determining the restricted ecosystem function of some Pacific island stream communities.

Few field studies of litter breakdown in Pacific island streams are available for comparison with our data. In Hawaii, Larned (2000) also found slow litter breakdown rates (k ranged from 0.007–0.024) and no endemic shredders. Indeed, the one shredder in Hawaii that did have a significant effect on litter breakdown was the exotic crayfish *Procambarus clarkii* (Larned et al. 2003). Our results can also be compared with published studies from other tropical islands. In a study of macroconsumer control on litter breakdown in a Puerto Rican river, March et al. (2001) found that the effect of macroconsumers depended on position along the river continuum (which controlled macroconsumer community composition). At low-elevation sites, where only *Macrobrachium* spp. were abundant, no effect of macroconsumer exclusion was observed. Only at the high-elevation site, where the shredding shrimp species *X. elongata* was common, was a treatment effect of macroconsumer exclusion found. Small or mixed effects of *Macrobrachium*-dominated shrimp communities on litter breakdown have also been seen in mainland tropical streams (e.g., Rosemond et al. 1998). Our Pacific island study at a low-elevation site also suggests an insignificant role of *M. lar* in litter breakdown. Macroconsumers in the Yela River might play a more important role at high-elevation sites where *M. latimanus* and several atyid shrimps are more abundant. As was seen in Puerto Rico, species identity and location along the stream continuum might be important in determining the relative role of macroconsumers in litter breakdown.

Importance of intact Pacific island stream communities

In some aspects, the Yela River is typical of perennial streams on Pacific high islands in that it is high-gradient; has relatively low dissolved N:P ratios, low insect richness and biomass; and is dominated by amphidromous macroconsumers. In contrast, the Yela River is atypical of Pacific island streams in that no anthropogenic structures (e.g., dams and roads) currently affect the migration of its freshwater fauna, and no flow diversions, no introduced aquatic species, no significant human harvest of species, and no landuse alterations occur in the catchment. The near-pristine nature of the Yela River watershed makes it extremely valuable for 2 reasons. First, a thorough knowledge of the structure and function of relatively intact river systems such as the Yela River might guide regional government agencies when assessing the effects of human activities and subsequently might aid them when developing strategies to mitigate the effects of human disturbance (e.g., Benstead et al. 1999). Second, as more data on the structure and function of stream communities become available from oceanic islands, it will become possible to ask broader ecological questions and to test the applicability of theory derived from continental sites on oceanic islands. The extreme simplicity of Pacific island stream communities makes them particularly valuable for comparative field studies that investigate relationships between biodiversity and ecosystem function. However, this work will be possible only through continued conservation of intact and undisturbed stream sites throughout the Pacific region.

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