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Ecosystem structure and function vary across stream order in Yosemite Valley

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Ecosystem structure and function vary across stream order in Yosemite Valley

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in

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by

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The Thesis of Stephanie Sueni Li is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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ABSTRACT OF THE THESIS

Ecosystem structure and function vary across stream order in Yosemite Valley

by

Stephanie Sueni Li

Master of Science in Biology

University of California San Diego, 2020

Professor Jonathan Shurin, Chair

Freshwater ecosystems have less surface area than the oceans but play an outsized role in the global carbon cycle. Organic matter produced in situ or entering as terrestrial detritus may accumulate in sediments, be respired and released as CO_2 to the atmosphere, or exported to the ocean. Aquatic decomposition of terrestrial detritus, periphyton primary productivity, benthic invertebrates (decomposers and grazers), and invertebrates that emerge from rivers contribute to the transport of carbon both downstream and between the terrestrial and aquatic ecosystems. I asked how decomposition rate, primary productivity, benthic macroinvertebrate biomass, and emergent macroinvertebrate biomass change with stream order in Yosemite Valley and El Portal, California, USA. In Summer 2019, I collected data at 19 sampling sites in the Merced River and its tributaries (Tenaya Creek and Yosemite Creek). Along with my main variables – decomposition rate, periphyton growth rate, benthic invertebrate biomass, and emergent invertebrate biomass – I considered environmental factors – elevation, temperature, and waterflow velocity. I found faster leaf decomposition at lower elevation and higher temperatures. Also, decomposition declined marginally with increasing invertebrate biomass. Other fluxes and stocks showed no relationship to stream order. Low elevation, high order rivers may therefore become more heterotrophic and release more CO_2 to the atmosphere as a result of faster mineralization of allochthonous organic material without apparent compensatory increases in photosynthetic uptake. How the balance of photosynthesis and respiration in ecosystems will respond to climate change is one of the major unknown feedbacks in forecasting the future course of carbon accumulation.

INTRODUCTION

Although freshwater ecosystems take up a much smaller surface area of the world than the ocean, freshwater ecosystems have a significant role in the global carbon cycle by storing carbon in freshwater sediments, exporting it to the atmosphere or the ocean (Cole et al., 2007). Freshwater bodies were once thought to be a way to passively transport carbon from land to ocean. In reality, freshwater plays an active role in the carbon cycle by respiring and storing carbon in addition to exporting it to the ocean. Carbon enters the water cycle through rivers and lakes as aquatic photosynthesis or terrestrial detritus, remains in the sediment, or leaves as runoff to the ocean or respiration to the atmosphere. Depending on the magnitude of these different pathways, aquatic ecosystems can be either a net source or sink of carbon to the oceans or the atmosphere.

Freshwater ecosystems are configured as a hydrological network where water flows from high elevation to low elevation. The river continuum concept (Vannote et al., 1980), describes predictable physical changes in lotic freshwater ecosystems across a gradient of stream order from small, high elevation, low order streams that flow into large, low elevation, high order rivers. Changes in the physical environment and supplies of different resources lead to shifts in community composition of organisms such as macroinvertebrates (Bae et al., 2003; Miller & Stout, 1989) and fish (Lotrich, 1973; Townsend et al., 2003), ecosystem processes (Jonsson & Malmqvist, 2000; Naiman et al., 1987; Rasmussen et al., 2010), and flux of organic matter (Benfield et al., 2000; Beilby et al., 1980; Naiman & Sedell, 1980; Webster & Meyer, 1997) across stream order. Low order streams contain mainly coarse particulate organic matter (CPOM), such as large wood or vegetation, (Weigelhofer & Waringer, 1994) and may have low light to support photosynthesis due to shading in forested watersheds (Naiman & Sedell, 1980).

Light levels may increase at high stream orders as riverbeds become wider and less influenced by shading (Naiman & Sedell, 1980). In addition, fine particulate organic matter (FPOM) may increase due to in-stream processing (Naiman & Sedell, 1979). Communities of organisms ranging from bacteria (McArthur et al., 1992) and algae (Wellnitz & Rader, 2003) to invertebrates (Bae et al., 2003) and fish (Paller, 1994; Platts, 1979) may vary along the stream continuum, although shifts depend on a variety of local environmental features. These environmental changes over the river system are likely to affect decomposition rates, primary productivity, macroinvertebrate biomass, and macroinvertebrate export biomass.

Organic matter flows into and out of streams in several forms. Terrestrial leaves falling in the stream and decomposing allows for the input of terrestrial organic materials and nutrients into the aquatic stream. Conners and Naiman (1984) found that leaf litter falling into streams is exponentially higher in low order streams rather than high order streams since there is more tree coverage at low order streams as opposed to the more open high order rivers. Decomposition supports production in stream food webs by releasing nutrients that increase primary production (Xiong & Nilsson, 1997), and by supporting growth of detritivorous animals and microbes including bacteria and fungi. Experimental studies that excluded leaf litter from streams saw strong bottom-up effects where there was a decline in abundance and/or biomass of benthic invertebrates (Wallace et al., 1997). There is no consensus in the literature on how decomposition rates change with stream order as some studies have found that decomposition rates are highest in low order streams (Cortes et al., 1995; Melillo et al., 1983), some have found rates are highest at high order streams (Hill et al., 1992) , and others have found no change in decomposition rate over stream order (Tiegs et al., 2009). Environmental factors have been shown to affect decomposition rate, which include temperature (Facelli & Prickett, 1991; Vogt et al., 1986) and water flow (Xiong & Nilsson, 1997). Biotic factors also affect decomposition rate, including leaf structure (Chamier, 1987; Meentemeyer, 1978; Vogt et al., 1986) and presence of invertebrates (Kominoski et al., 2011; Wallace et al., 1982) and microbes (Chamier, 1987; Jackrel et al., 2019). Symons and Shurin (2016) also found that presence of insectivorous fish predators in lakes at low elevation can decrease the density of invertebrates that decompose detritus, therefore slowing down decomposition rate. Since all of these factors are likely to change across stream order, decomposition rate is also expected to depend on elevation. Since higher temperature is known to increase metabolic of invertebrates, bacteria, and fungi – the biggest aquatic decomposers – I expect decomposition rate to increase at high order streams, which are also warmer.

Aquatic primary production is another source of organic matter in stream food webs. Algae may be larger contributors to food webs than in temperate rivers and streams compared to topical latitudes (Davies et al., 2008). Studies have also seen that net photosynthesis is inversely related to water velocity (Madsen et al., 1993). Similar to decomposition, no clear consensus exists on how primary production varies across stream order. Munn et al. (1989) saw that periphyton growth rates were highest at low order streams, while Seyfer & Wilhm (1977) saw chlorophyll-a and ash free dry mass highest at high order streams. Temperature, light, nutrient supply, and grazing have a significant influence on primary production and are expected to vary with stream order. Hornick et al. (1981) found that there is higher primary production downstream and that the abiotic factors that have the greatest influence on periphyton primary production rates are light, stream flow, and inorganic carbon. In agricultural streams, temperature and light are limiting factors on periphyton growth as opposed to nutrients (Munn et al., 1989). Overall, primary production depends on light and nutrients, which may covary as shading increases and phytoplankton or aquatic plants become abundant when nutrients are high.

Benthic macroinvertebrates play a large role as shredders/decomposers of large organic matter, filter feeders of algae, grazers of periphyton, and predators. Benthos includes molluscs and crustaceans that remain aquatic for their entire lives, as well as insect larvae that emerge out of the stream and live in the terrestrial habitat as adults. Also, terrestrial invertebrates fall into streams and provide an important resource for aquatic predators like fish. This flow of energy into the stream is especially important during seasons when aquatic productivity is low due to shading by terrestrial vegetation (Nakano et al., 2001). The river continuum concept (Vannote et al., 1980) also states that aquatic invertebrate communities change across stream order with shredders dominating low order streams and filter feeders dominating high order streams. Ecoregions are the most important factor in determining the community of benthic invertebrates with more invertebrate taxa in mountain streams than in plains streams (Tate & Heiny, 1995). Benthic invertebrate biomass also varies seasonally (Eckert et al. 2020). Since many benthic macroinvertebrates are only aquatic as larvae, these invertebrates eventually get exported from the aquatic habitat to the terrestrial habitat by emerging out of the stream as adults. This export of aquatic organic materials and nutrients into the terrestrial habitat supports terrestrial predators that consume emerging macroinvertebrates. A study where emerging insects were experimentally excluded found that the presence of aquatic insects allowed the predatory lizards to shift their diet from terrestrial to aquatic (Sabo & Power, 2002). Riparian spiders also rely on emerging insects as a food source where an experiment removed emerging insects and saw more spiders in areas with emerging insects as opposed to without (Marczak & Richardson, 2007). The transfer of invertebrates into and out of streams varies seasonally with energy flow going in both directions between terrestrial and aquatic (Nakano & Murakami, 2001). A literature review has shown both aquatic and riparian consumers rely on the land-freshwater resource exchange (Richardson et al., 2010). Jackson et al. (2020) studied the Tuolumne and Merced Rivers in Yosemite National Park and found that birds and bats relied more heavily on emergent aquatic insects for nutrients during dryer years. Movement of biomass between streams and their watersheds therefore depends on stream order, latitude, and season. If invertebrate biomass is under bottom-up control, then I expect it to be positively correlated with primary production and/or detritus supply with food availability limiting the invertebrate population. Alternatively, if invertebrates exert strong top-down control on periphyton and/or litter decomposition, then I expect to see negative correlations with invertebrates controlling the food supply.

In this study, I asked how decomposition of terrestrial detritus, periphyton growth (primary productivity), benthic macroinvertebrate biomass, and export of emergent macroinvertebrate biomass change with stream order within the Merced River and its tributaries in Yosemite Valley and El Portal, California, USA. In mountainous areas like the Sierra Nevada range, stream order varies greatly within a short geographic distance. As such, it is possible to observe changes in ecosystems over large gradients in stream order within comparable climate conditions. I sampled pools and fluxes of benthic periphyton, decomposition of terrestrial leaf litter, standing biomass and export of invertebrates among 19 sites between two low-order streams and a mid-order river over two months during summer of 2019. My goal was to ask how important components of stream food web vary with elevation in a mountain region.

METHODS

Sampling Sites

I collected samples for five weeks, from July 12 to August 17, 2019, in Yosemite Valley, Yosemite National Park, California, USA along the Merced River and its tributaries of Yosemite Creek and Tenaya Creek. I also collected samples along a section of the Merced River farther downstream in El Portal, California, USA. I recorded measurements across 19 sampling sites that were categorized into four regions — Tributary, Upper Merced, Lower Merced, or El Portal — with five sites in each region except for El Portal which had four sites. I selected sites that were harder for the public to access or supposed to be closed off to the public to discourage tampering and loss of sampling gear. I aimed for all sites to have similar substrate (sandy) and tried to avoid shading by trees whenever possible by placing sampling materials in the middle of the stream.

I measured four ecosystem structures and functions – decomposition rate, periphyton growth rate, benthic invertebrate biomass, and emergent invertebrate biomass – along with environmental factors – water flow velocity, elevation, and water temperature.

Categorizing stream order

While my sampling sites technically span over two stream orders, the four stream regions act as “pseudo stream orders” with Tributary, Upper Merced, Lower Merced, and El Portal in order from lowest to highest stream order. Because sites have large elevation gradient (827 meters difference between the highest and lowest sites), we would also expect a large gradient in physical and biological factors. Since stream order encapsulates the idea of physical and biological changes across a gradient, I used the four categories to replace stream order. Along with this same idea, elevation of sampling sites is also used as a proxy for stream order.

Ecosystem structures and functions

To measure rates of decomposition, I dried terrestrial willow tree leaves (*Salix sp.*) outdoors in the sun for two days. Leaves were weighed out to 1.50g ± 0.01g and placed in closed mesh bags with a mesh size of 0.0255mm^2. Five bags were placed on the streambed at each site. Each week for five weeks, a single bag was removed from the stream and frozen until samples were processed in the lab. In the lab, I rinsed leaves with DI water, dried them at 45℃ for 48 hours, and weighed for dry mass. I then combusted leaves in a muffle furnace at 550℃ for 24 hours and weighed them again to determine ash mass. I calculated ash-free dry mass by subtracting ash mass from dry mass and plotted this data against time as a scatterplot for each site and calculated a regression line. The slope of the line was considered the rate of decomposition over time for each site. Although decomposition is typically calculated as an exponential decay function, a linear plot was a better fit for my data likely because I did not measure decomposition rate for long enough that it began to decline. Decomposition rate was not measured at four sites because tampering by the public led to the disappearance of sampling gear.

To measure periphyton growth rates, I placed five unglazed ceramic 23.04 mm^2 tiles on the streambed at each site. Each week, I removed one tile, scrubbed it with a toothbrush, and rinsed it with stream water. I filtered the water through a 25mm diameter glass microfiber filter (GF/F). I froze filters and kept them in the dark until I processed them in the lab. I repeated this process once a week for five weeks. In the lab, I extracted chlorophyll from filters in 100% methanol for 24 hours. I analyzed samples with a fluorometer (Turner Designs Trilogy Laboratory Fluorometer) using the extracted chlorophyll-a non-acidification module. I then calculated chlorophyll concentration on the tile by using solvent volume, tile area, and percentage filtered. I plotted chlorophyll concentration against time as a scatterplot for each site and calculated a regression line. The slope of the line was considered the periphyton growth rate over time for each site. Periphyton growth rate was not measured at eight sites because tampering by the public led to the disappearance of sampling gear.

Benthic invertebrates were collected with Surber sampling nets and vigorously agitating sediment using a hand trowel within a 100 cm^2 upstream frame for one minute. I rinsed the sample through three layers of sieves (mesh sizes of 1 mm, 500 µm, and 250 µm), removed invertebrates by hand, recorded by insect order for abundance data, and removed and preserved in ethanol. The samples were collected at each site once a week for four weeks. In the lab, I measured the body length of a random subset of individuals of each taxon, calculated average body length for each order present, converted to biomass using $\text{Biomass} = 0.019\text{Length}^{2.46}$ (Smock, 1980), and multiplied by abundance.

To measure biomass of invertebrates emerging out of the river, I mounted petri dishes on four-foot poles and sprayed with a sticky commercial substance used to trap insects (Tanglefoot). Eight petri dishes were mounted at each site. In the lab, I categorized insects into size categories, converted to biomass using $\text{Biomass} = 0.019\text{Length}^{2.46}$ (Smock, 1980), and multiplied by abundance. Insect emergence was measured once on August 17 after the traps had been deployed for seven days.

Environmental Variables

To measure flow velocity, I used a handheld flow meter (General Oceanics, Inc., Miami, FL, USA) for 30 seconds at a 1-foot depth in the water column. I collected samples once a week for four weeks as close as possible to the site where other measurements and samples were taken.

Later in the study, flow was too low to measure at some of my sampling sites. In that case, I measured flow a few feet away towards the middle of the river, where flow was higher. Flow velocity was averaged over the four sampling weeks.

Elevation data available from U.S. Geological Survey, National Geospatial Program. Water temperature was measured every 60 minutes for five weeks using a HOBO Pendant data logger (Onset Computer Corporation, Bourne, MA, USA).

Statistics

Linear regression analysis was used to examine changes in ecosystem rates and structures in relation to elevation and measured environmental variables. Analysis of variance with a post-hoc Tukey Honest Significant Difference test was used to compare ecosystem rates between the four stream regions. Analysis was conducted in R version 3.6.3 (R Core Team, 2020).

RESULTS

The decomposition rates ranged among sites from the slowest decomposition, a loss of 0.021 g per week, to the fastest decomposition, a loss of 0.093 g per week (Fig. 1). The periphyton growth rates ranged among sites from 0.008 to 0.392 $\mu g/mm^2$ per week (Fig. 2). Benthic invertebrate biomass ranged among sites from 0.020 to 1.03 mg total over five sampling periods. Emergent invertebrate biomass ranged among sites from 0.003 to 0.052 mg total over a one-week sampling period.

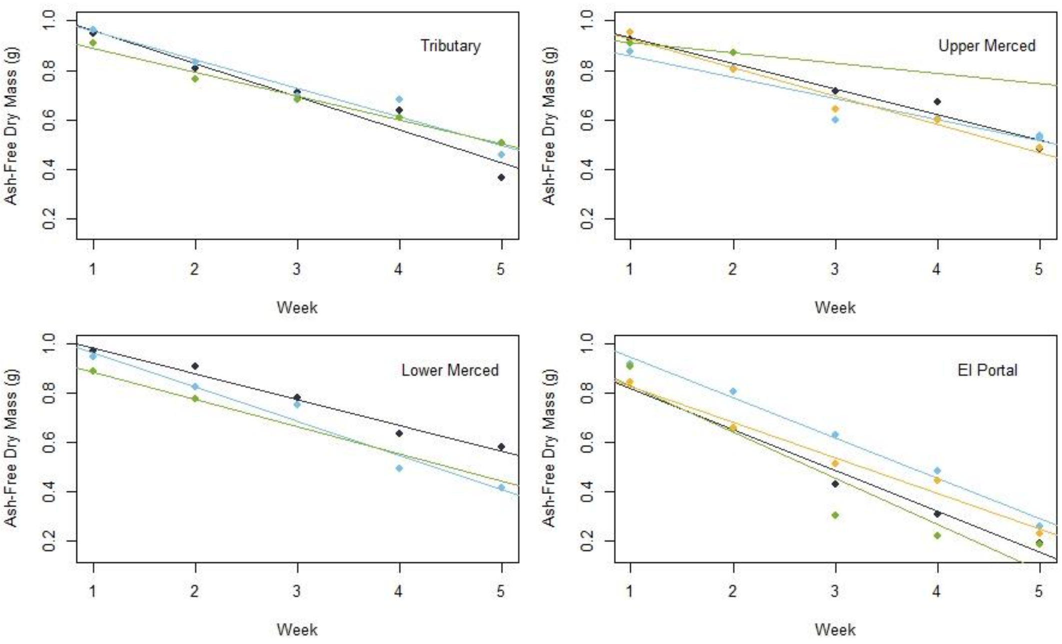

Figure 1: Scatterplots showing ash-free dry mass of decomposing leaf litter across the five-week sampling period. Each graph is a different stream region. Regions ordered from lowest to highest stream order: Tributary, Upper Merced, Lower Merced, El Portal. Each data point represents one mesh bag of dried leaves left in the river for that number of weeks. Line of best fit is the decomposition rate for a sampling site. Colors to differentiate between different sampling sites within each region.

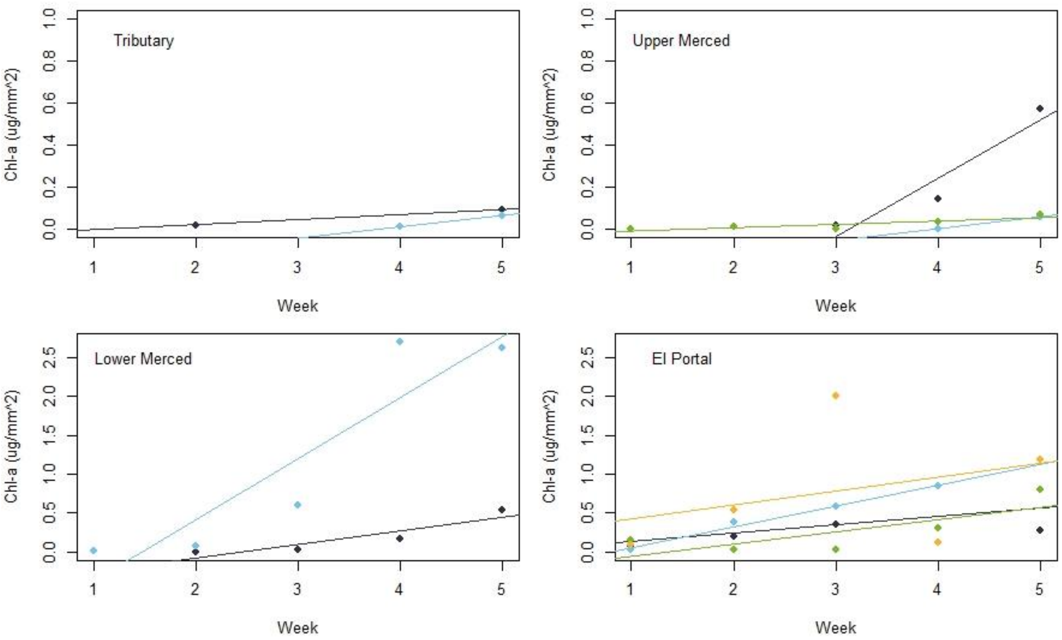

Figure 2: Scatterplots showing chlorophyll-a concentration of periphyton across the five-week sampling period. Each graph is a different stream region. Regions ordered from lowest to highest stream order: Tributary, Upper Merced, Lower Merced, El Portal. Each data point represents a tile left in the river for that number of weeks. Line of best fit is the periphyton growth rate for a sampling site. Colors to differentiate between different sampling sites within each region.

I found that none of the ecosystem structures or functions – decomposition rate, periphyton growth rate, benthic invertebrate biomass, and emergent invertebrate biomass – showed a significant relationship with one another by linear regression (Fig. 3). Decomposition rate was marginally negatively related to emergent invertebrate biomass (Fig. 3, $F_{1,\,12} = 4.456$, $p = 0.0564$, $R^2 = 0.21$).

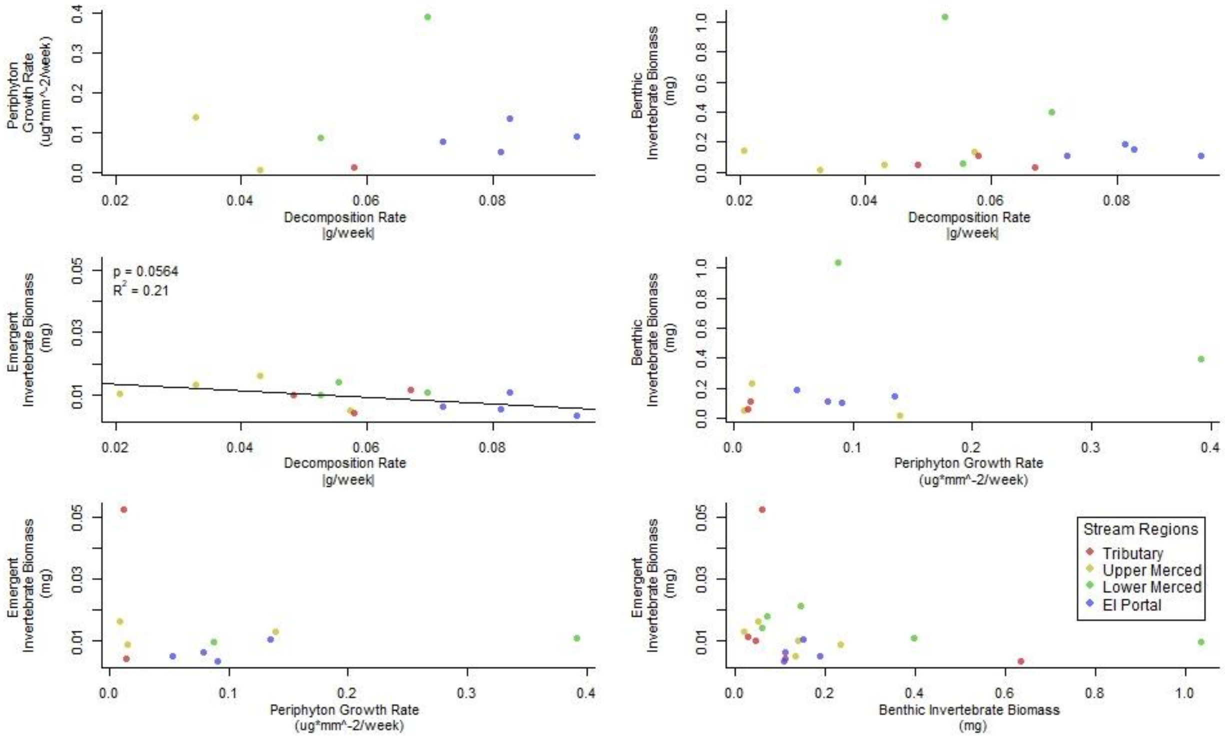

Figure 3: Scatterplots of all combinations of the ecosystem rates and functions (decomposition rate, periphyton growth rate, benthic invertebrate biomass, emergent invertebrate biomass). All relationships are insignificant, but decomposition rate is marginally negatively related to emergent invertebrate biomass ($p = 0.0564$). Decomposition rate is the absolute value of the slope of change in mass over time of terrestrial detritus.

Using elevation of sampling sites as a proxy for stream order, I found faster decomposition rates at lower elevation (Fig. 4, $F_{1,\,12} = 14.97$, $p = 0.0022$, $R^2 = 0.518$) and at higher temperatures (Fig. 4, $F_{1,\,10} = 13.74$, $p = 0.0041$, $R^2 = 0.537$), but no relation with water flow velocity. Also, decomposition rates differed across stream regions (Fig. 5, $F_{3,\,10} = 10.02$, p =

0.0023) with faster decomposition rates at El Portal sites than Upper Merced sites (p = 0.0013). Periphyton production, benthic invertebrate biomass, and biomass of emergent insects were not significantly related to flow velocity, elevation, or temperature by linear regression (Fig. 4).

I also found that water temperature and elevation were inversely related ($F_{1,\,10}$ = 219.5, p << 0.001, R^2 = 0.952). Average flow velocity was not significantly related to elevation.

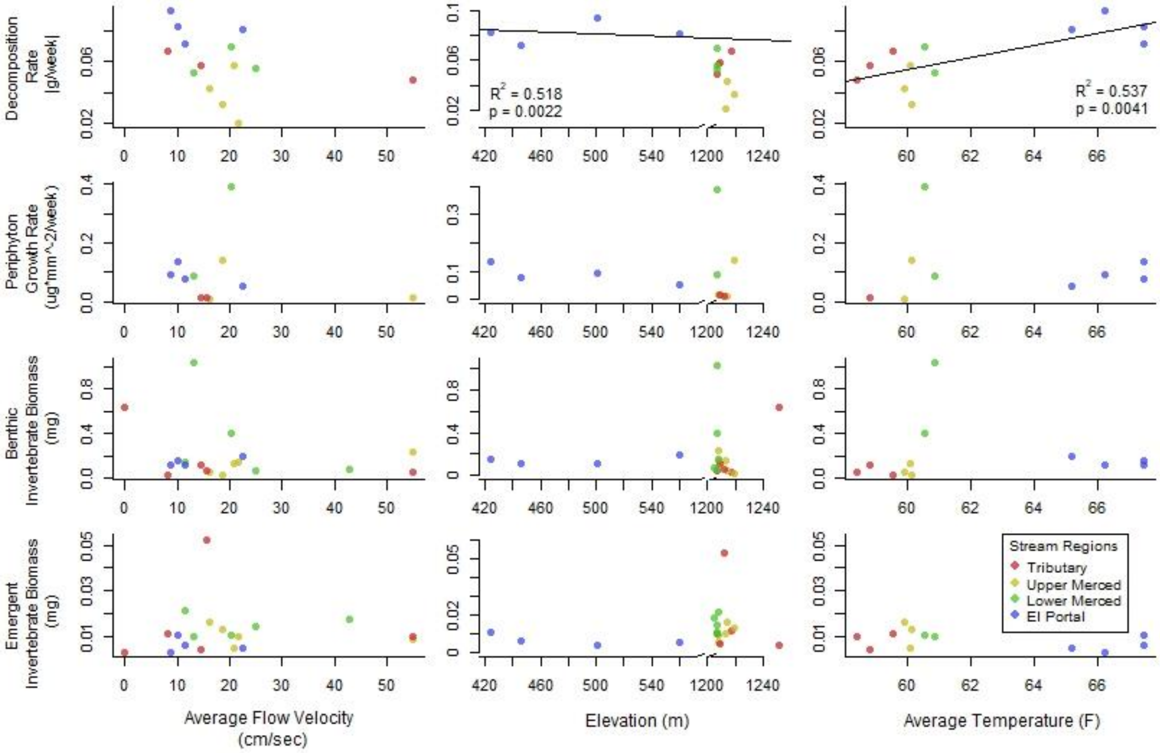

Figure 4: Scatterplots showing relationship between ecosystem structures and functions with environmental factors – water flow velocity, elevation, and water temperature. Each data point represents a sampling site with the color of data points representing different stream regions. Line of best fit drawn on statistically significant graphs. Decomposition rate is shown as the absolute value of the slope of change in mass over time of terrestrial detritus.

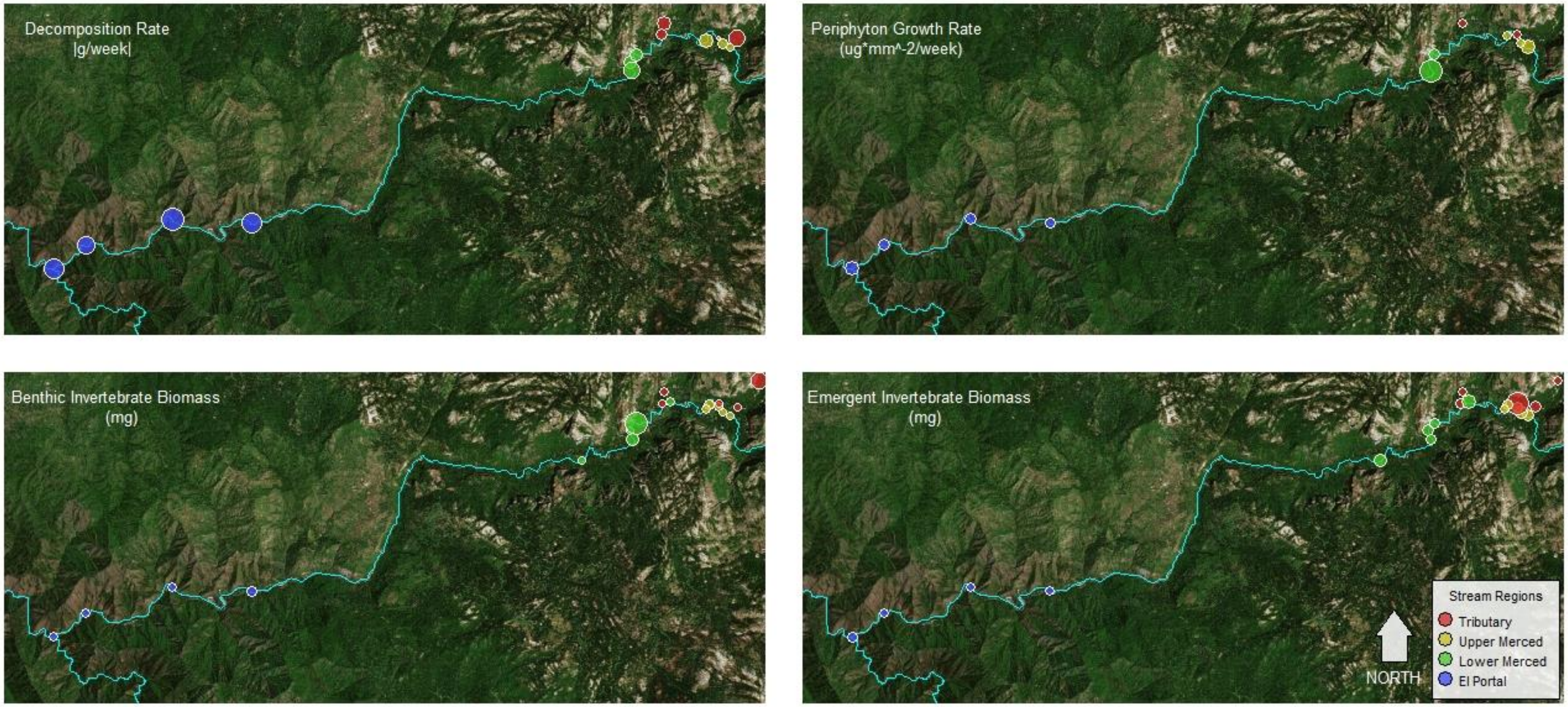

Figure 5: Four satellite-view maps of Yosemite Valley and El Portal. The blue line represents Merced River. Each data point represents a sampling site. Size of dots are based on value of the variable with larger dots representing a greater measurement. Color of data point indicates the stream region.

DISCUSSION

My thesis revealed increased decomposition of terrestrial detritus in higher order streams at lower elevations, but no changes in other measured ecosystem pools or fluxes with stream order. These results indicate that environmental gradients associated with elevation, such as temperature, result in faster remineralization of terrestrial organic matter or conversion of CPOM into FPOM without apparent changes in *in situ* primary production or the biomass or emergence of aquatic invertebrates. Low elevation, high order rivers may therefore become more heterotrophic and release more CO_2 to the atmosphere or export less organic carbon downstream as a result of faster mineralization of allochthonous organic material without apparent compensatory increases in photosynthetic uptake. My results indicate that, at the scale of Yosemite Valley, only decomposition shows significant changes with elevation and temperature.

As expected, since temperature is a main driver of decomposition, decomposition rates increased with warmer water temperatures. Greater metabolic activity of shredding invertebrates, heterotrophic bacteria, or fungi at high temperature may explain the elevated decomposition rate at low elevations. On the one hand, the river continuum concept states that shredders dominate low order streams like the ones in my study, leading me to believe decomposition rates would be higher at low order streams. I found the opposite pattern indicating that environmental controls on decomposition may supersede changes in invertebrate community composition. I found faster decomposition rates with increasing stream order in Yosemite Valley, which corroborates the findings of Hill et al. (1992). Even so, my finding differs from other studies that found the opposite to be true (Cortes et al., 1995; Melillo et al., 1983) or that did not find a relationship at all (Tiegs et al. 2009). The contradictory results may indicate that regionally specific environmental conditions like climate, water chemistry, geology, or biotic communities may determine the relationship between decomposition and stream order. In the scope of this study, physical factors like high water discharge rate or temperatures may explain the faster break down of terrestrial detritus.

Previous studies have not reached a clear consensus on the relationship between primary productivity and stream order. For example, while Naiman & Sedell (1980) found that primary productivity was highest at high order streams, Munn et al. (1989) contradicted the study and found that periphyton growth rates were highest at low order streams. Additionally, Naiman & Sedell (1980) found that net community production (NCP) was positively related to stream order. I found no relationship between stream order and periphyton growth rate. Primary productivity may vary with a number of different environmental factors that I did not measure, notably light availability and nutrients. My findings could be a result of the fact that factors like light, nutrients, and grazing change in non-linear ways across stream order and therefore could change in a way that counteract each other. Although leaf litter decomposition releases nutrients in the water, which increases periphyton growth, I did not see a relationship between decomposition rate and periphyton growth. The increase in nutrients downstream may be counteracted by greater light absorption in a deeper water column or due to greater amounts of suspended fine particulate material (Vannote et al., 1980), resulting in no net change in photosynthesis.

Although benthic invertebrates play a substantial role in decomposing leaf litter in streams, I did not find a relationship between the two in my study. Not seeing a relationship could indicate that other unmeasured factors, such as microbial activity, affect decomposition rates play a significant role in the decomposition of leaf litter at my sampling sites. If invertebrate biomass is under bottom-up control, then I expect it to be positively correlated with primary production and/or detritus supply. Alternatively, if invertebrates exert strong top-down control on periphyton and/or litter decomposition, then I expect to see negative correlations. The lack of correlation may indicate either that both processes are simultaneously important, or that other environmental factors like the number of higher order predators such as fish may control invertebrate biomass. My study does not allow for me to distinguish these possibilities and future research may be able to determine the factors that control stream invertebrate biomass in Yosemite Valley. Studies have found that fungi populations are denser at high order (Graça et al., 2001). If this is true for my study, then fungi could play a large role as decomposers and be driving the higher decomposition rate that I saw downstream. Also, since decomposers have been shown to dominate the low order (Graça et al., 2001; Vannote et al., 1980), it would be interesting to learn more about how functional groups of invertebrates vary across stream order in my study.

Emergent invertebrate biomass was the only variable that I found to have a marginal relationship to decomposition rate. I found a faster decomposition rate with a lower emergent biomass. The cause of this relationship is unknown and statistical support for this finding is weak, therefore a functional relationship between emergence and decomposition may be false. Emergence was unrelated to in-stream invertebrate biomass, indicating that standing stock of invertebrates is unrelated to the amount of export to the watershed. Emergence was also unrelated to elevation, suggesting that unknown factors determine the flux of aquatic biomass to the forest. Since emergent insect biomass is lowest in the summer and highest in the spring (Nakano & Murakami, 2001), the biomass I saw in the summer may not have covered a large enough gradient to see an effect. Conducting this study in the spring could see a larger gradient and different results.

How the balance of photosynthesis and respiration in ecosystems will respond to climate change is one of the major unknown feedbacks in forecasting the future course of carbon accumulation. Variation in ecosystem fluxes along natural gradients such as elevation or latitude may guide my expectations. My study found that of two ecosystem rates (decomposition and primary production) and two standing stocks (invertebrate biomass and emergence), only decomposition varied consistently with elevation. The increased decomposition at low elevation is expected if temperature is a major factor in leaf litter breakdown. With an increase of heterotrophic processes (decomposition) downstream, but no change in photosynthesis, I expect this system to be more heterotrophic at low elevation. Over this gradient I studied, the amount of CO_2 given off may increase, but the amount of CO_2 uptake does not change. Faster degradation of particulate organic matter in warmer, high order streams may result in greater release of CO_2 to the atmosphere at lower elevations in montane environments.

To further understand primary productivity in Yosemite Valley, future studies should examine how light and nutrients vary across stream order. It would also be interesting to learn how fungal and microbial biomass vary with decomposition rate in Yosemite Valley to better understand what organisms take part in decomposition in the Merced River. The role of higher order predators, like fish or river otters, in stream ecosystem processes may also explain some of the unaccounted-for variation shown in my thesis.

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