





EFFECTS OF LAND USE, STREAMBED TOPOGRAPHY AND MACROINVERTEBRATES ON DECOMPOSITION RATES OF Syzygium guineense (Willd, 1828) AND Eucalyptus saligna (Smith, 1797) LEAF LITTER IN THE KAMWETI RIVER, KENYA

Master of Science Thesis

by

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has not been submitted or presented for examination in any institution.

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This thesis has been submitted for examination with	h our approval as University supervisors.

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DEDICATION

To my father, the late Idirisa Makame, and mum, Mwanasiti Hamadi, for their inspiration and moral support toward education.

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ABSTRACT

Land use change from forests to agricultural land, has been reported to negatively affect stream ecosystem structure and function. Riffles and pools exhibit heterogeneity in physical, chemical, and biological characteristics, which in turn may affect stream function. However, information on the effects of land use and streambed topography on the functioning of tropical streams, is still limited. Leaf litter decomposition, a key ecosystem process that links trophic interactions, was used in this study as a functional indicator of stream ecosystem. This study was set up to assess the influence of land use and streambed topography on decomposition rates of Syzygium guineense and Eucalyptus saligna leaf litter in the Kamweti River, Kenya. The decomposition experiment was conducted following the standard litter bag technique. A total of 400 coarse-mesh (0.5mm) litter bags were used to enclose 5 ± 0.05 g of each plant species leaf litter, incubated in the selected sites and thereafter 5 replicates of litter bags were randomly retrieved after an interval of 1, 3, 8, 14, 21, 28, 35, 42, 49 and 56 days of incubation. Also, the maximum leaching time and leaf nutrient content were evaluated in the laboratory. Triplicate benthic and drift macroinvertebrates samples were collected to help answer the question whether there was a similarity between leaf litter-associated, drifting and benthic macroinvertebrates. Benthic and drift macroinvertebrates were sampled using 0.5mm kick net and 0.1mm drift net sampler, respectively. Decomposition rates were estimated using the negative exponential decay model. Linear Mixed effect Models were used to evaluate the effects of land use and streambed topography on leaf litter decomposition rates, macroinvertebrates and physico-chemical parameters. Syzygium guineense consistently had significantly higher concentrations of all the nutrient parameters than Eucalyptus saligna, except for total nitrogen. The maximum leaching time for both plant species was estimated to be 12 hours. Forested sites (Syzygium = 0.0269 ± 0.004 , Eucalyptus = 0.0408 ± 0.004) had higher decomposition rates than agricultural sites (Syzygium=0.0205 ± 0.004, Eucalyptus $=0.0269 \pm 0.006$), although not significantly different(p> 0.05). Riffle habitats had significantly higher decomposition rates (p < 0.05) than pool habitats across the two land uses. Eucalyptus sp had significantly higher decomposition rate than Syzygium guineense (p=0.0007) across the land use. Macroinvertebrates colonizing the leaf litters were largely more similar to those from benthic zone, but different to those from drift. Overall, Syzygium sp was found to be a betterquality leaf litter nutritionally than Eucalyptus sp. Streambed topography had a significant effect on leaf litter decomposition than land use. Eucalyptus afforestation should be discouraged as it contributes leaf litter with a lower nutritional value to stream ecosystems. Conservation and management efforts should be directed to the local scale factor as opposed to only riparian and catchment factors.

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LIST OF ABBREVIATIONS AND ACRONYMS

AFDM Ash Free Dry Mass

APHA American Public Health Association

CL Collectors

DO Dissolved Oxygen

FFGs Functional Feeding Groups

GF/C Glass Fibre Filter/Coarse

LMM Linear Mixed effect Models

NMDS Non-Metric Multidimensional Scaling

PCA Principal Component Analysis

PRD Predators

RCC River Continuum Concept

SCR Scrappers

SDC Serial Discontinuity Concept

SHR Shredders

SRP Soluble Reactive Phosphorus

TDS Total Dissolved Solids

TN Total Nitrogen

TP Total Phosphorous

TSS Total Suspended Solids

QHA-S Qualitative Habitat Assessment Score

CHAPTER ONE INTRODUCTION

1.1 Background information

Freshwater ecosystems are among the most threatened ecosystems on the Earth by anthropogenic disturbances (Reid *et al.*, 2019; Vörösmarty *et al.*, 2010). These anthropogenic disturbances include riparian zone deforestation, habitat fragmentation and degradation (Sundar *et al.*, 2020), land use intensification, agricultural activities (Overbeck *et al.*, 2015), pollution (Mayer-Pinto *et al.*, 2015), urbanization, mining and damming (Dirzo *et al.*, 2014). These disturbances are the main drivers of ecological degradation through increased nutrients and fine sediment concentrations (Carpenter *et al.*, 2011), changes in flow regimes, discharge and stream channel structure (Leal *et al.*, 2016), which results in the reduction of stream habitats and consequently negatively affecting the biodiversity of aquatic biota (Firmiano *et al.*, 2017).

Rivers and streams are energetically linked with their riparian zones, which supply allochthonous organic matter from their riparian vegetation. Riparian vegetation controls availability of light for autochthonous producers, and ensures ecosystem processes such as fine substrate retention, microclimate modification and regulation (Neres-Lima *et al.*, 2017; Tank *et al.*, 2010). Additionally, they provide shading through canopy cover hence limiting direct solar insolation on streambed and consequently decreases water temperature and thereby limiting autochthonous production (Riis *et al.*, 2020). Furthermore, allochthonous leaf litter input by riparian vegetation into streams constitutes important shelter and feeding resources for aquatic organisms (Ligeiro *et al.*, 2020). However, riparian zones have experienced a lot of anthropogenic disturbances, including pollution, deforestation, conversion from forested to agricultural land, and replacement of native riparian plant species with exotic ones (Ferreira *et al.*, 2006; Hladyz *et al.*, 2011). These anthropogenic disturbances influence environmental factors such as soil erosion and sedimentation as well as input of nutrients and toxic substances into streams and rivers. These, in turn, affect macroinvertebrates and microorganisms density and thus influencing leaf litter decomposition rates in such systems.

Land-use changes along the riparian zones have led to the replacement of natural vegetations with agricultural practices, exotic plant species and pasture land (Hladyz *et al.*, 2011). These changes can modify the quality and quantity of leaf litter that enters into stream ecosystems (Silva-junior *et al.*, 2014), light and temperature regimes which in turn increase nutrient inputs and primary production. Given that allochthonous organic material is an important energy source for heterotrophic organisms (Vannote *et al.*, 1980), change in the type

and quantity of leaf litter inputs into streams can influence microorganisms and macroinvertebrate assemblages. This occurs through modifying the abundance and distribution of different taxa and functional feeding groups (Encalada *et al.*, 2010; Masese *et al.*, 2014), hence causing a change in the leaf litter decomposition process (Casotti *et al.*, 2015). Moreover, land use change, such as conversion of forests to agricultural land, subjects rivers and stream ecosystems to habitat loss, increased lateral inputs of nutrients, fine and dissolved organic and inorganic matter, higher light conditions and increases water temperature (Rasmussen *et al.*, 2012). Accordingly, these can have adverse consequences not only for stream biodiversity, but also for important ecosystem processes, such as leaf litter decomposition (Fugère *et al.*, 2018; Silva-Junior *et al.*, 2014).

Litter decomposition is the breakdown of dead organic material into progressively smaller sized particles until the structure can no longer be recognized, and organic molecules are mineralized to their prime constituents: CO₂, H₂O and mineral components (Cotrufo *et al.*, 2010). Leaf litter decomposition is driven by the chemistry and intrinsic traits of leaf litter, availability and activity of detritivorous organisms and water physico-chemical characteristics (Kominoski & Rosemond, 2012; Tank *et al.*, 2010), as well as the result of physical abrasion by water currents (Graça *et al.*, 2001; Hieber & Gesner, 2002). The chemistry and intrinsic characteristics of leaf litter influences the colonization rate and activity by microbial organisms and macroinvertebrate shredders (Ligeiro *et al.*, 2010).

Leaf litter decomposition generally occurs through a system of sequential processes. The first one being the passive leaching of soluble compounds such soluble sugars. This process is mainly completed between the first 24-48 hours after immersion into water and can result in a loss of up to 30% of the original mass, depending on the plant species. The other processes are microbial colonization and conditioning (Gessner & Chauvet, 1994), colonization and fragmentation by macroinvertebrate shredders and physical abrasion by stream water currents (Graça et al., 2005). Once immersed in the stream, leaf litter is quickly colonized by microorganisms which breakdown the leaf constituents, and thus enhance leaf litter decomposition (Gessner et al., 2010). The microbial colonization or conditioning process reduces leaf toughness and makes the leaf litter more palatable by invertebrate shredders, promoting the leaf litter decomposition process (Gessner et al., 2010; Hieber & Gessner, 2020). However, macroinvertebrate shredders are mainly affected by land use changes along the riparian zone. Moreover, the conversion of forests to agricultural and pasture land, and the replacement of native riparian vegetation by exotic tree species can result to a reduction in quality and quantity of leaf litter input (Allan, 2004). Consequently, the macroinvertebrate

shredder abundance can be reduced by food limitation, poor leaf litter quality, thereby affecting leaf litter decomposition (Graça *et al.*, 2015).

Clearing of native riparian vegetation, increased input of pollutants and sediment supplies as well as flow regime alterations in stream channels are negative impacts due to land use, all of which can affect stream structure and functioning (Allan, 2004). On the other hand, differences in substrate composition, width, depth and flow velocity promote heterogeneity in the structure of these lotic ecosystems (Cushing & Allan, 2001). This can result in the formation of areas with distinct physico-chemical characteristics, commonly referred to as mesohabitats such as riffles and pools. These habitats exhibit heterogeneity in physical, chemical, and biological characteristics (Brown & Brussock, 1991; Herbst et al., 2018), which in turn may affect stream ecosystem processes such as leaf litter decomposition. Riffles experience higher current velocities while pools have lower current velocities (Montgomery & Buffington, 1997). Due to these differences and other factors such as flow conditions, depth, width, oxygen concentrations, sediment and organic matter retentiveness, riffles and pools exhibit heterogeneity in both structural and functional composition of macroinvertebrates. Additionally, the distinct characteristics of riffle and pool habitats may lead to variation in the composition, abundance, richness, and local distribution of macroinvertebrates (Brown & Brussock, 1991) and microbial organisms which in turn may affect leaf litter decomposition. The macroinvertebrates that colonize leaf litter may originate from drift or from the benthic zone. However, there is limited comparative information on the structural and functional composition of leaf litter-associated macroinvertebrates and those in drift and benthic zones.

Kamweti River has been greatly affected by rapid and increased land use change. Native vegetation and natural forests in the Kamweti River area has been completely cleared for cultivation and replaced with exotic tree species, thereby affecting the stream ecosystem functioning. Furthermore, human related activities appear to be expanding more rapidly. Few studies carried out in tropical streams have shown that riparian zone deforestation to give room for agricultural activities affects the ecological integrity through reduction in water quality and modification of benthic macroinvertebrates communities (Bücker *et al.*, 2010). Similarly, research from montane freshwater ecosystems (Astudillo *et al.*, 2016) have shown that conversion of forests to agricultural areas can alter detritivorous consumer assemblages and hence reduce the decomposition rates of leaf litter (Encalada *et al.*, 2010). Despite the rapid land use change, the relationship between land use, stream water physico-chemical variables, macroinvertebrates communities and ecosystem functions in the Kamweti River has not been well studied. Therefore, there is need to understand the influence of land use on the functioning

of the Kamweti River by using leaf litter decomposition process as the indicator of stream function. The aim of this study was to evaluate the effect of land use and streambed topography (i.e., pool and riffles) on decomposition rates of two plant species leaf litter, one native plant species, *Syzygium guineense*, and one exotic plant species, *Eucalyptus saligna*. Additionally, this study aimed at evaluating the nutritive value of the plant species leaf litter and to establish the similarity between macroinvertebrates assemblages in the benthic zone, drift and the ones associated with leaf litter.

1.2 Statement of the problem

Exotic tree species can change the stream ecosystem functioning through modified energy transfer dynamics. Kamweti River ecosystem has experienced rapid and increased land use change, human encroachment to riparian land together with replacement of riparian natural forests and vegetation with exotic tree species. Native riparian vegetation and forests in the Kamweti region have been entirely claimed for cultivation and replaced with exotic tree species, with only a small portion in the Mt. Kenya national park where natural vegetation is still intact. The relationship between land use and streambed topography on litter processing in streams has not been fully studied for tropical streams. It is also not well known whether topography of the streambed alone is more important in comparison to the overall land use in dictating stream functioning. Therefore, this study offers an opportunity to test how land use and streambed topography (riffles and pools) influence leaf litter processing for better management of tropical streams.

1.3 Objectives

1.3.1 General objective

To evaluate the role of land use, streambed topography and macroinvertebrates on decomposition rates of litter in tropical riverine ecosystems, a case study of the Kamweti River, Kenya.

1.3.2 Specific objectives

- (i) To establish the nutrient content (soluble reactive phosphorous, nitrate, nitrite, ammonium, total phosphorous and total nitrogen) and maximum leaching time of *Syzygium guineense* and *Eucalyptus saligna* leaf litter.
- (ii) To determine the effect of land use and streambed topography (pools and riffles) on decomposition rates of *Syzygium guineense* and *Eucalyptus saligna* leaf litter.

(iii) To establish whether the macroinvertebrates associated with leaf litter decomposition are taxonomically similar to those from benthos and drift.

1.4 Hypotheses

- (i) Ho_{1:} There are no significant difference in the nutrient content (soluble reactive phosphorous, nitrate, nitrite, ammonium, total phosphorous and total nitrogen) and maximum leaching time of *Syzygium guineense* and *Eucalyptus saligna* leaf litter.
- (ii) Ho₂: Land use and streambed topography do not significantly affect the decomposition rate of *Syzygium guineense* and *Eucalyptus saligna* leaf litter and macroinvertebrates assemblage.
- (iii) Ho₃: The macroinvertebrates colonizing the leaves are not taxonomically similar to those from benthos and drift.

1.5 Justification

Land use change, economic and landscape developments along riparian zones have led to replacement of natural riparian vegetation with exotic plant species, such as Eucalyptus species along the Kamweti River. These anthropogenic activities (e.g., land use) interfere with the normal functioning of streams through modification of environmental factors, quality and quantity of leaf litter input as well as macroinvertebrate shredders and microorganisms. Consequently, these changes may affect leaf litter decomposition process. Overall, provision of ecosystem services such nutrient cycling, water quality purification, are limited in such ecosystems which have been influenced by anthropogenic activities. For sustainable management of such ecosystems, continuous assessment of the effect of land use changes along riparian zones is needed. The study of leaf litter decomposition at the catchment (land use) and biotope (riffles and pools) scales along Kamweti River will offer an opportunity to identify factors that affect stream ecosystem function at different spatial scales. Therefore, this study could help in answering key questions such as "how does land use and streambed topography (riffles and pools) influence stream ecosystem function and how can they be integrated between and within spatial scales to assess stream ecosystem function. The results will provide more knowledge on the effects of land use on the stream function, inform the society on the actions to be taken for conservation, and recommendation for best management practices.

CHAPTER TWO

LITERATURE REVIEW

2.1 Leaf nutrient content, and macroinvertebrate shredders participation in leaf litter decomposition

Most of the chemical and structural compounds of plant leaves play an important defensive role (Biasi et al., 2003). For example, chemical compounds such as lignin and cellulose concentrations increase the leaf toughness, hence making it rigid, thereby preventing them from herbivory, and consequently from detritivores (Ardón & Pringle, 2008). Other compounds, such as polyphenols, have a repellent effect hence inhibit detritus colonization by microorganisms and macroinvertebrates (Hepp et al., 2008). Furthermore, plant leaf litter with a high concentration of secondary metabolites and a high carbon: nitrogen ratio could be less attractive to macroinvertebrate shredders and, therefore would affect its decomposition process (Graça & Cressa, 2010). However, high concentration of nitrogen in leaf litter enhance microbial activity (Menéndez et al., 2011), thereby making the leaf litter more palatable and attractive to macroinvertebrates shredders (Graça & Cressa, 2010), and consequently increasing the leaf litter decomposition rate. As a result, the interaction between leaf litter characteristics and macroinvertebrate colonization has a direct effect on the decomposition rate of plant species leaf litter. Consequently, different riparian plant species leaf litter could have different dynamics of decomposition and colonization by microorganisms macroinvertebrates when they fall into streams. Therefore, replacement of native riparian zones plant species with exotic ones may have a significant effect on the litter dynamics (Ehrenfeld, 2010).

Plant leaf traits are important in examining how they respond to their environment and conversely how they affect stream ecosystem processes, such as litter decomposition (Violle et al., 2007). Since leaf litter play a key role in the exchange of nutrients and energy between plants and their environment, interspecific differences in many plants species leaf litter has been given a particular attention (Wright et al., 2004). Variability in the characteristics of leaf litter within species have been less emphasized, possibly due to the existing evidence that supports the idea that intraspecific variations are much smaller than interspecific differences (Roche et al., 2004). Intraspecific variability in leaf characteristics can modify organic matter dynamics in streams. Previous research has found variability in the decomposition rates of leaves among populations, plants and leaves (Silfver et al., 2007). These variations have been attributed to a difference in litter quality, which is thought to affect utilization of leaf by detritivore consumers (Cadisch & Giller, 1997). This intraspecific variation in leaf

characteristics can in turn, influence the growth, biomass, abundance, and rates of nutrient assimilation of microbial and macroinvertebrates detritivores (Compson *et al.*, 2018). Moreover, stream detritivore consumers can adapt locally to intraspecific variation in riparian plant species and become more efficient at decomposing leaf litter inputs from certain trees.

Additionally, leaf litter decomposition rate is also controlled by intrinsic nitrogen and phosphorous content of the leaf litter (Gessner & Chauvet, 1994). Furthermore, changes in leaf litter characteristics because of terrestrial herbivory could also influence intraspecific variation in the leaf litter decomposition rates. Damages to plants by herbivores such as grasshoppers and aphids often stimulates chemical defences and reduced leaf nutrient content, hence lowering the decomposition rate (Choudhury, 1988). For example, in an experiment with the red alder, Jackerel and Wootton (2015) reported a reduced in-stream leaf litter decomposition rate of up to 42 %, relative a control set in an experiment with red alder leave where a simulated herbivory was mimicked by punching holes in leaves and applying a chemical signalling herbivore damage. Therefore, variation in plant leaf litter characteristics within species phenotypic plasticity in leaf chemistry and palatability due to herbivory could also be an important source of variation in leaf litter decomposition rates within species.

2.2 Land use, streambed topography and leaf litter decomposition rates

Leaf litter decomposition rate in stream is affected by both natural and anthropogenic factors. Natural factors influencing variation in leaf litter decomposition rate include temperature, water nutrient concentration, characteristics of litter, abundance and composition of microorganisms and macroinvertebrate shredders (Boyero *et al.*, 2011). On the other hand, anthropogenic disturbances that affect these variables could also influence leaf litter decomposition rates. For instance, land use often significantly affects leaf litter decomposition rate through its effect on stream nutrient concentrations, sedimentation, and abundance of detritivorous consumer i.e., macroinvertebrates and microorganisms (Sponseller & Benfield, 2001; Woodward *et al.*, 2012).

Land use change has resulted to the removal of riparian vegetation along most tropical streams. Removal of riparian vegetation and conversion to agricultural lands has led to loss of allochthonous organic matter input; an important energy source especially for small, forested headwater streams (Júnior & Callisto, 2013). Studies have shown that changes in the riparian conditions lead to variations in the aquatic organisms through alteration of environmental factors such as dissolved oxygen concentration and increased nutrients concentrations

(Gonçalves *et al.*, 2012). Furthermore, changes in riparian vegetation modify the dynamics, distribution and breakdown of allochthonous organic matter (Encalada *et al.*, 2010).

Globally, increased human population growth has led to agricultural intensification, making it a dominant and expanding land management practice (Tilman et al., 2001), occupying 40% of the Earth's surface (Graeber et al., 2015). Riparian land conversion from native forest to agricultural land is worrying, particularly in tropical regions where it is occurring at an alarming rate (Gibbs et al., 2010). This results into adverse consequences not only to stream biodiversity but also to stream ecosystem processes (Laurance et al., 2014). A case in point is the shifting of the relative importance from allochthonous to autochthonous energy pathways which supports abundant consumer production in forested headwater streams with high leaf litter inputs (Vannote et al., 1980; Wallace et al., 2015). Furthermore, agricultural activities cause a variety of environmental changes that act as stressors for stream ecosystems, such as loss of riparian shading, increased water temperature, and decreased inputs of allochthonous organic matter. As a result, these can affect stream biodiversity and assemblages (Allan, 2004), increased nutrient concentrations from fertilizer run off, sedimentation and the presence of pesticides (Cornejo et al., 2019). Evidence from research in temperate streams show that increased nutrient concentration stimulate microbial decomposition (Ferreira et al., 2006; Rossi et al., 2019) but impair macroinvertebrate assemblages and macroinvertebrate-mediated decomposition, similar to fertilizers, pesticides, siltation and sedimentation (Chará-Serna & Richardson, 2018). Conversion of forests to agricultural lands has resulted to major changes in riparian vegetation, hence adversely affecting the diversity, quality and quantity of leaf litter inputs into streams (Casotti et al. 2015; Silva-Junior et al. 2014). Additionally, absence of riparian vegetation result to increased water temperature, sedimentation and nutrient run off, thereby influencing microbial and macroinvertebrates activity on leaf litter decomposition (Encalada et al., 2010). For example, increased water temperature (Davidson et al., 2006), and moderate nutrient enrichment levels (Woodward et al., 2012) stimulate metabolic activities, hence enhancing biological decomposition activity, whereas increased sediment result into high water turbidity, thereby causing a reduction in light penetration hence impairing autotrophic production (Mercer et al., 2014).

Human settlement and agricultural practices can increase turbidity through nutrient loads, sediment, or both (Henley *et al.*, 2000). Soil erosion resulting from agricultural irrigation and overland flows over the impervious surfaces of urban area can as well produce sediments (Wu *et al.*, 2012). Nutrient enrichment can lead to eutrophication and algal blooms hence an

indirect source of turbidity (Schindler, 2006). Increased sediment load and its resultant turbidity can adversely affect benthic macroinvertebrates communities (Dlamini *et al.*, 2010). For instance, sedimentation and settlement of fine particulate matter can negatively affect benthic macroinvertebrates by filling the interstitial pore spaces in the sediments thus inhibiting interstitial water movement (Gordon *et al.*, 2004).

Previous studies evaluating the impact of agriculture and exotic tree replacement (e.g., Eucalyptus) on leaf litter decomposition rates in streams between forested and disturbed sites showed ariability in leaf litter decomposition rates ranging from reduced (Casotti et al., 2015) to increased leaf litter decomposition (Jinggut et al., 2012), or to no difference between both sites (Foster et al., 2011). However, similar studies have also shown contrasting results between forested and agriculturally impacted sites with decomposition rates primarily dependent on the leaf litter quality under study (Cizungu et al., 2014; Ferreira et al., 2006). For example, streams in tropical regions have often reported lower decomposition rates in agricultural land use compared with forested streams (Encalada et al., 2010; Silva-Junior et al., 2014). Additionally, Fugère et al. (2018) reported lower leaf litter decomposition rates in agricultural streams than in forested streams within protected watersheds. This pattern contrasts with the often-higher leaf litter decomposition rates in agricultural sites in other regions, where increased nutrient concentration from agricultural activities stimulated the decomposition rate (Allan, 2004). Furthermore, key macroinvertebrate shredder species in the region are sensitive taxa that are mainly eliminated from agricultural sites (Fugère et al., 2016). In tropical streams, leaf litter decomposition is mainly driven by microorganisms with a minor contribution of macroinvertebrate shredders (Boyero et al., 2011). In such a scenario, the effect of agriculture on leaf litter decomposition rates could be expected to be lower than those from temperate streams. However, this may not always be the case, because the role of the detritivore consumers may be important especially at high attitudes (Yule et al., 2009) or in some other biogeographic areas (Boyero et al., 2015).

Streams in a watershed are viewed through a hierarchical framework that depicts spatial and temporal variations within and among streams along riverscapes (Allan, 2004). Stream habitat types (i.e., riffles and pools) differ in velocity, substrate types and water depth (Sponseller & Benfield, 2001). Riffles and pools are known to have distinct conditions based on flow conditions, depth and slope of the water surface (Brussock *et al.*, 1985). Generally, streams that have step-pool sequences or cobble substratum are said to be more stable and thus can provide stable and diversified habitats for benthic macroinvertebrates and microorganisms. Step-pool sequences can enhance the flow resistance and stabilize streambed and banks hence

have considerable ecological importance. The intensity and frequency of anthropogenic disturbance vary between pools and riffles and hence may have a significant impact on their community structures (Resh *et al.*, 1988). Therefore, studying the role of streambed topography is of great significance for stream ecologists to better understand the physical, chemical, and biological processes taking place in the streambed.

2.3 Colonization patterns of leaf litter by macroinvertebrates

Macroinvertebrates recolonization of stream substrate after a disturbance is said to be one of the key processes that structure communities in rivers and streams (Boyero & Bosch, 2004). This process is generally fast beginning within one hour of disturbance and end in as few as 30 days (Lake & Schreiber, 1991). This process depends largely on organisms that arrive with the drift (downstream movement of organisms within the water column), from communities in surrounding areas, and by recruitment through oviposition (Encalada & Peckarsky, 2006). Several studies have shown that drift is the main mechanism of benthic organisms redistribution in streams (Fenoglio *et al.*, 2004).

Macroinvertebrates colonization is a species-specific process which is influenced by physical, chemical, and biological factors. For example, connectivity, hydrological characteristics (e.g., shape, length and substrate), water quality parameters, including temperature, discharge, depth, and light, seasonality (Jones, 2010), associated food sources, competition, and predation are among important factors which influence species colonization. Other factors such as in-stream habitat, diversity and complexity including substrate characteristics, riffle-pool sequences, and the presence of woody debris, can have a positive effect on macroinvertebrates colonization by increasing diversity and abundance of organisms (Lepori *et al.*, 2005). Similarly, resources from upstream, riparian vegetation and allochthonous organic matter inputs play key roles in macroinvertebrates colonization and community structure (Wallace *et al.*, 2015).

Drift species composition may significantly influence benthic community dynamics. This may occur either by reducing density of benthic species that are more prone to drift, which affects the local community structure, composition, and abundance, or through continuous settling of macroinvertebrates in the streambed (Townsend & Hildrew, 1976). Study by Townsend and Hildrew (1976) reported that 82% of colonization was due to drift in an English stream while Williams and Hynes (1976) found 41.1% of colonization in a Canadian stream experiment was due to drift. However, Resh *et al.* (1981) reported contrasting results in a Californian stream, where recolonization by the Trichoptera after ecological succession was

mainly due to vertical migration, with drift contributing only 5% of the colonists. In temperate areas, where the role of drift in benthic colonization is well studied and documented (Mackay, 1992), it has been established that at small temporal scales, majority of the colonizing organisms come from drift (Williams & Hynes, 1976).

The role of drift in recolonization processes of tropical systems has been studied (Melo & Froehlich, 2004). These studies have shown that recolonization of macroinvertebrates in tropical rivers varies among riffles, but not among river sections, and that the type of organisms that recolonize substrate depends on both drift from upstream and surrounding patches at the local scale (Boyero & Bosch, 2004). Different species traits and life history adaptations of the benthic organisms can also influence recolonization at new or disturbed substrate. According to Ríos-Touma *et al.* (2012), macroinvertebrates colonization in the tropics is very fast, and that no difference in community metrics between day 7 and day 25 of recolonization experiment was found. However, it was reported that most common taxa showed marked differences between mesohabitats, and consequently, community metrics values were higher in fast-velocity areas. Similar results have also been reported in the high Andean streams of Ecuador (Jacobsen, 2005). In conclusion, studies suggest that variability of flow, discharge and drift response play a key role in macroinvertebrate colonization and consequently in the structuring of macroinvertebrates communities in different mesohabitats of tropical streams.

2.4 Synthesis of leaf litter decomposition process in streams

Land use change affect both the structure and functioning of stream ecosystems (Allan, 2004). The negative impacts of land use on stream environmental factors which in turn affect the aquatic communities are closely related to the stream ecosystem processes, such as leaf litter decomposition, has been well studied both in temperate (Hladyz *et al.*, 2011) and some lowland tropical streams (Silva-Junior & Moulton, 2011). Land use change (i.e., the conversion from natural forest to human-dominated land) typically degrades freshwater ecosystems due to agricultural activities, dams and irrigation and channel construction (Silver-Junior & Moulton, 2011; Silver-Junior *et al.*, 2014). These changes can result in the reduction of riparian and canopy cover which in turn affect the shading effect and consequently increasing stream water temperature, and lower allochthonous leaf litter inputs, which can affect stream biodiversity and assemblages (Junqueira *et al.*, 2016). Furthermore, land use changes causes an increase nutrient enrichment and resuspension, and clearing of riparian vegetation (Silva-Junior, 2016). The changes can lead to a reduction in the quality of physical habitat and consequently affecting species richness and diversity of organisms, in turn affecting the functioning of the ecosystem.

Leaf litter decomposition, a biological process, regulated by detritivorous consumers i.e., microbial decomposers and macroinvertebrates shredders (Hieber & Gessner, 2002; Webster & Benfield, 1986), is highly sensitive to land use changes (Ferreira *et al.*, 2015). Leaf litter decomposition in streams may be influenced by a group of factors. First, leaf litter decomposition may be affected by the chemical and inherent characteristics of the plant species leaf litter. Evidence from previous studies have shown that macroinvertebrate shredders activity and consequently leaf litter decomposition are positively affected by leaf nutrient content, and negatively affected by secondary metabolites and leaf toughness (Ferreira *et al.*, 2012; Graça, 2001).

Secondly, leaf litter decomposition can be influenced by stream water physicochemical factor. For example, increased water temperature, dissolved oxygen concentration, flow velocity, and concentrations of nitrogen and phosphorous usually have a positive effect on the leaf litter decomposition rate (Ferreira & Chauvet, 2011). Increased concentration of nitrogen and phosphorous from agricultural run-off typically increase leaf litter decomposition rate by stimulating increase of microorganism biomass (Krauss et al., 2011). Conversely, high water temperature and nutrient concentration causes high oxidation rates of dissolved organic matter in agricultural sites, thus reducing the oxygen availability. As a result, activity of detritivores consumers is decreased (Medeiros et al., 2009), thereby negatively affecting leaf litter decomposition rates. Furthermore, high water temperature in agricultural streams increases passive leaching of soluble compounds and can stimulate microbial activities (Ferreira & Chauvet, 2011), consequently, increasing leaf litter decomposition rate. Low dissolved oxygen concentration can also reduce sensitive macroinvertebrates taxa, such as, Trichoptera, which has been reported to be the main shredder group in tropical streams (Couceiro et al., 2007). Low pH affects leaf litter decomposition rate by reducing the diversity of decomposer communities (Petrin et al., 2007). Similarly, variability in stream discharge can positively increase leaf litter decomposition rates where high stream flows increase physical fragmentation of leaves through abrasion as well as the downstream fluxes of nutrients and carbon to microorganisms and other biota, thereby increasing leaf litter mass loss (Gonçalves et al., 2006). Increased stream flow due to altered channel dynamics can cause physical abrasion of leaves in streams (Paul et al., 2006).

Lastly, fallen leaf litter is quickly colonized by microorganisms and start the decomposition process by producing enzymes (Fenoglio *et al.*, 2006). These microorganisms, in turn, promotes colonization by macroinvertebrate shredders that consume the leaf litter, hence increasing the decomposition rate (Boyero *et al.*, 2012; Graça & Cressa, 2010).

Microorganisms condition leaf litter hence enhance the quality and palatability of the litter for macroinvertebrate shredders by breaking down the secondary metabolites such as cellulose and lignin. Also, they take nutrients from the water column and incorporate them into the biofilm, thereby increasing leaf nutrient content, especially nitrogen and phosphorus (Haapala *et al.*, 2001).

Leaf litter assimilation by macroinvertebrates shredders is influenced by the inherent characteristics of leaves and by microbial conditioning (Graça, 2001). The relative importance of microorganism and macroinvertebrates shredders on leaf litter decomposition seems to vary across regions (Eggert & Wallace, 2003). The importance of macroinvertebrates and microbial decomposer communities in litter processing in the tropical streams is still unclear. Some previous studies suggest that an important difference between temperate and tropical systems is the low abundance of macroinvertebrate shredders in the tropics (Gonçalves et al., 2004). However, other previous studies have shown that macroinvertebrate shredders have an important role in leaf litter processing in some tropical systems (Cheshire et al., 2005) and according to (Rincón and Martínez, 2006), tropical macroinvertebrate shredders are selective feeders. Thus, the role of aquatic macroinvertebrate shredders in leaf litter processing is still unclear in the tropical systems. Positive correlation between leaf litter decomposition rates and macroinvertebrate shredders abundance has been reported in temperate streams (Sponseller & Benfield, 2001), and a positive relationship between macroinvertebrates shredder species richness and breakdown rates has been detected in field studies (Lecerf et al., 2005) and some laboratory experiments (Jonsson & Malmqvist, 2000).

The River Continuum Concept (RCC; Vannote *et al.*, 1980) describes the longitudinal variations in the relative abundances of macroinvertebrates functional feeding groups (FFGs). It predicts that collector-gatherers and shredders co-dominate the benthic communities in the forested small headwater streams that receive large amount of allochthonous leaf litter input from the riparian vegetation. In contrast to RCC predictions, a lack of macroinvertebrate shredders has been reported in streams outside the north temperate region, e.g., in Australia and New Guinea (Yule, 1996), tropical Asia (Dudgeon, 2000), East Africa (Dobson *et al.*, 2002), and the Neotropics (Greathouse & Pringle, 2006). However, there are reports of abundant macroinvertebrate shredders in leaf packs and benthic samples from tropical Australian streams (Cheshire *et al.*, 2005).

Most studies on leaf litter decomposition have been done in temperate deciduous forests (Graça, 2001), but the few studies that have been done in the tropical streams have shown that leaf litter decomposition rates can also be affected by land use (Rosemond *et al.*, 2002). For

example, the conversion of native forests to agriculture, pasture or urbanization can change stream flow, pH, increase nutrient concentrations and water temperature, and can reduce macroinvertebrates densities (Allan, 2004). Consequently, changes in these stream variables can affect the leaf litter decomposition dynamics in different manners. Leaf litter decomposition rates can be slower in rural streams compared to forested streams due to the stream habitat simplification on aquatic organisms as well as negative effects of sedimentation (Rasmussen et al., 2012), or due to low abundance of macroinvertebrate shredders (Encalada et al., 2010). Additionally, agricultural activities lead to the removal of riparian vegetation, thereby causing a decrease in leaf litter input and an increase in light conditions (Encalada et al., 2010). The low leaf litter input in agricultural streams can negatively affect availability of food resources for macroinvertebrate shredders whereas the increased light condition increases water temperature and algal biomass hence may alter the structure and functioning of the ecosystem (England & Rosemond, 2004). Therefore, there is need to evaluate the relationship between land use, streambed topography and leaf litter decomposition rates, since such information is either scanty or still not well understood in the tropical region, especially in Kenyan streams.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study area and sites

3.1.1 Study Area

Kamweti area is located approximately at latitude 0° 20′S to 0° 22′S and longitude 30° 25′E to 37° 30′E on the southern slopes of Mount Kenya (M'Erimba *et al.*, 2018) (Figure 1). The landscape is well-preserved, with rocky Afro-montane forests at higher elevations and diverse riverine forests in the valleys. Several rivers and streams pass through the area, the main ones being the Kavute River and Kamweti River, both of which are main tributaries of the Thiba River, which drains into the Tana River. These are permanent rivers that provide water to various parts of the region and serve as the primary source of water for irrigation region (Kaberia, 2007).

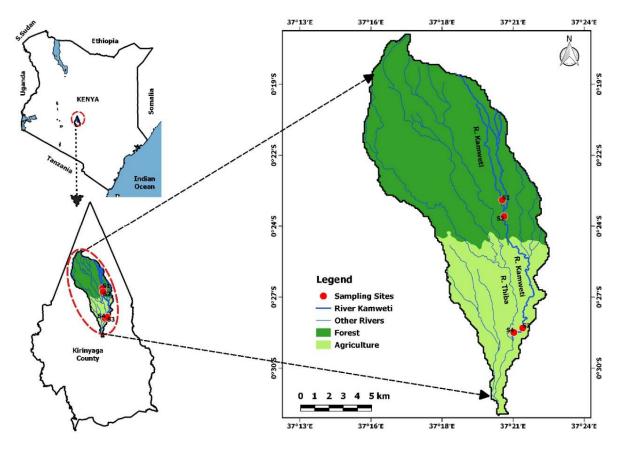


Figure 1: A Map of Kamweti River catchment showing the sampling sites (Source: Modified from Google map).

Kamweti area experiences a cool and moist climate, with a mean temperature ranging from 16.6 to 20.1°C. The area experiences bimodal rainfall pattern with two peaks, one from March to May (long rains) and the other from October to December (short rains) (Figure 2), and an annual rainfall ranging from 800 to 2150 mm. The area is characterized by tertiary volcanic rocks, and the soils are generally brown loams derived from volcanic ash. In some areas, soils are reddish and have smeary consistence. Brown loamy soils absorb a lot of water and have a high organic matter content (5 to 20%). The soils are fertile, well-drained, and have a stable soil structure.

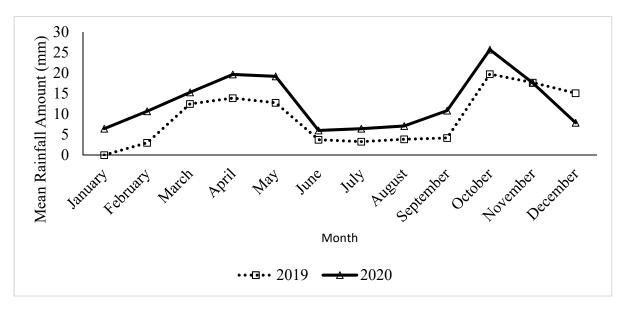


Figure 2: Mean monthly rainfall between 2019 and 2020 along the Kamweti area (Data Source: Kamweti Agricultural Training Centre).

Upstream of the Kamweti River has been restricted to natural vegetation, with the forest consisting of both natural and exotic species. *Eucalyptus saligna* and *Cupressus lusitanica* are the most common exotic plant species, while *Rapanea melanophloeos* and *Syzygium guineense* are the most common indigenous plant species. Downstream of the Kamweti River, the area has been cleared for cultivation of both subsistence farming and *Eucalyptus plantation*. The cultivated area has an average elevation of 1700 meters above sea level (Kaberia, 2007).

3.1.2 Description of study sites

Site 1(Riffle, Forest) was located at latitude of $00^{\circ}23'17.8''$ S and longitude of $037^{\circ}20'24.0''$ E. The site had a mean width of 6.46 ± 0.349 m, and depth of 0.23 ± 0.03 m (Table 1). It had a canopy cover of 60% comprising of indigenous riparian vegetation. The

riparian vegetation was dominated by native tree species, shading the instream areas, and is mainly composed of *Tabernaemontania stapfiana* (Apocynaceae family), *Syzygium guineense* (Myrtaceae family) and *Neubotonia macrocalyx* (Euphorbiaceae family). Both banks were stable and intact with no sign of erosion. The sites had optimal epifaunal substrate, with minimum levels of embeddedness. The substrate composition was mainly made up of cobbles (50%), followed by boulders (30%), pebbles (15%) and lastly sand and gravel (5%). Water levels reaches both lower banks and minimal amount of substrate was exposed. There were neither signs of channelization nor dredging, the stream had normal pattern with a high frequency of riffles, and no human activities were observed in this site.

Site 2 (Pool, forest) was located at latitude $00^{\circ}24^{\circ}09.3^{\circ}S$ and longitude of $037^{\circ}20^{\circ}42.9^{\circ}$. The site had a mean width of 8.94 ± 0.52 m, and a mean depth of 0.37 ± 0.01 . The canopy cover was slightly lower compared to site one (about 55 %). Native riparian tree species dominates in this site, thereby providing shading into the streambed. The native tree species are similar to those found in site one; *Tabernaemontania stapfiana* (Apocynaceae family), *Syzygium guineense* (Myrtaceae family) and *Neubotonia macrocalyx* (Euphorbiaceae family). Both banks were less stable, and signs of erosion were observed. The sites had optimal epifaunal substrate, with minimum levels of embeddedness. The substrate composition was dominated by pebbles (40%), followed by cobbles (35%), boulders (15%) and lastly sand and gravels (10%). Similarly, water reaches both lower banks and minimal amount of substrate was exposed. There were neither signs of channelization nor dredging, and the stream had normal pattern with a suboptimal frequency of riffles. There were no human activities apart from water abstraction, about 100 m upstream of the sampling site.

Site 3 (Pool, agriculture) was located at latitude $00^{\circ}28'30.4"$ and longitude of $037^{\circ}21'16.7"$. The mean width and depth were 13.4 ± 0.6 , and 0.19 ± 0.04 , respectively. It had a canopy cover of about 50% with exotic riparian vegetation. The riparian vegetation was dominated by an exotic tree of *Eucalyptus saligna* along the banks. Sand and gravel substrates dominated the streambed (80%), followed by pebbles (10%) and cobbles and boulders covered 5% each. Both banks were less stable, and signs of erosion were observed. Marginal epifaunal substrate and a very high level of embeddedness was observed. Water reaches both lower banks and minimal amount of substrate was exposed. There were minimal signs of channelization and dredging, and the stream had normal pattern with a very low frequency of riffles. Human activities recorded at the site include, *Eucalyptus* plantation, subsistence farming (kales, yam, maize, and sweet potatoes) and tree logging.

Site 4 (Riffle, agriculture) was located at latitude $00^{\circ}29'31.6"S$ and longitude $0037^{\circ}21'16.7"$. The site had a mean width of 13.4 ± 0.6 m, and a depth of 0.19 ± 0.04 m. It had a canopy cover of about 33 % which composed mainly of exotic riparian vegetation dominated by *Eucalyptus* sp along the banks. Both banks were less stable, and signs of erosion were observed. The sites had marginal epifaunal substrate, with a very high levels of embeddedness. The substrate composition was mainly boulders (35%), pebbles (25%), cobbles (25%) and sand and gravel was the least with 15%. Water reaches both lower banks and minimal amount of substrate was exposed. There were minimal signs of channelization and dredging, the stream had normal pattern with a very low frequency of riffles. Crop farming (which included yams, banana, maize, and grass for fodder), and *Eucalyptus* plantation was evident on both sides of the riverbanks. Animal grazing and watering in the river coupled with domestic uses by neighbouring communities were also evident. Generally, in terms of quality habitat scoring, site 1 scored the highest value (98.5%) while site 4 scored the least (48%) (Table 1).This implies that site 1 was largely natural with few modifications, while site 4 was largely modified (Appendix 1).

3.2 Study design and sampling design

The study design adopted was the longitudinal study design, where repeated measurements were taken over a period of time. Purposive systematic random sampling design was used to select the sampling sites based on land use and streambed topography along the river (see figures 1a - d). Four sampling sites were selected, two in each land use based on the dominant biotope, either riffle or pool. The riffle and pool sites in each land use were approximately 100 meters apart to avoid the interactions and influence from each other. Simple random sampling design was used in data collection.

Table 1: Geographical position and habitat characteristics across the study sites in Kamweti River

	Forest		Agriculture	
Parameter	Riffle	Pool	Riffle	Pool
Altitude (m asl)	1810	1790	1540	1525
Latitude	00°23'17.8"	00°24'09.3"	00°29'31.6"	00°28'30.4"
Longitude	037°20'24.0"	037°20'42.9"	037°21'16.7"	037°21'11.7"
Width (m)	6.46 ± 0.349	8.94 ± 0.52	13.4 ± 0.6	5.00 ± 0.00
Depth (m)	0.23 ± 0.03	0.37 ± 0.01	0.19 ± 0.04	0.45 ± 0.16
Velocity (m/s)	0.19 ± 0.00	0.11 ± 0.03	0.19 ± 0.00	0.14 ± 0.03
Discharge (m ³ /s)	1.44 ± 0.13	0.44 ± 0.45	2.01 ± 0.24	0.65 ± 0.13
Substrate Composition				
% Boulders	30	15	35	5
% Cobbles	50	35	25	5
% Pebbles	15	40	25	10
% Sand and Gravel	5	10	15	80
% Canopy Cover	60	55	33	50
Slope				
Left Bank	10°-15°	20°-75°	35°-45°	40°-45°
Right bank	5°-10°	60°-65°	15°-25°	45°-50°
*QHA-S	98.5	90	48	59

^{*}QHA-Quality Habitat Assessment score



Figure 3(a-d): Sampling sites along Kamweti River (a-riffle, forested; b-pool, forested; c-pool, agricultural; d-riffle, agricultural).

3.2.1 Site characterization

Site characterization was conducted on the first day of sampling including assessing both in-stream and riparian conditions at each site as described by Kleynhans (1996) and Barbour *et al.* (1999). The bottom substrate was assessed visually during low water level, and categorized as 'boulders' (250 mm), 'cobbles' (60–250 mm), 'gravel' (10–60 mm), 'fine gravel' (2–10 mm), 'clay, sand and silt'(0.06-2mm), coarse organic matter (Mbaka *et al.*, 2015). Canopy cover and substrate embeddedness, a measure of the degree to which large particles (e.g., cobbles) are covered by fine sediment, was also assessed visually and then classified (Gordon *et al.*, 2004).

On each sampling day at each site, stream width, depth, current velocity, discharge, and selected physico-chemical parameters were determined. Stream width was measured with a

measuring tape on 5 transects at midpoints of 5 m intervals along the reach. On each transect, water depth was measured with a 1-m ruler at a minimum of 5 points (Masese *et al.*, 2014). Mean current velocity was measured at 60% of the total water depth with a mechanical Vale port flow meter model 0012/B (Richard & Gary, 2007) at every site (Figure 5a, b). Discharge was computed from velocity, width and depth data as described by Gordon *et al.* (2004).





Figure 4(a,b):Measurement of (a) flow velocity and (b)stream width and depth, in the study sites

3.2.2 Determination of physico-chemical variables of the stream water

Five replicates of water temperature (°C), electrical conductivity (μS/cm), total dissolved solids (mg/L), dissolved oxygen (mg/L) concentration, percentage oxygen saturation and pH, were measured *in situ* using a portable multisensor probe (HACCH-40d). In addition, five replicates of water samples for nutrient analysis were collected at each site using acid-washed bottles preconditioned with stream water. About 500 ml of water samples were immediately filtered through 0.45μm pore size pre-weighed glass-fibre filters (Whatman GF/C, pre-dried at 95°C, 12 h) within 10 h of sampling. Both the filtered and unfiltered water samples were put in a cooler box and transported to the laboratory.

Upon arrival of the samples at the laboratory, the unfiltered samples were used to measure total nitrogen (TN) and total phosphorus (TP) concentrations, while filtered samples were used to analyse ammonium (NH₄⁺), nitrite (NO₂⁻), nitrate (NO₃⁻) and soluble reactive

phosphorus (SRP). Nutrient concentrations were determined using the standard calorimetric methods (APHA, 2005). The concentrations were determined following the Lambert-Beer law, where a straight line is obtained when plotting absorbance versus concentration on mm graph paper, commonly known as the standard curve (Appendix 3). The final concentrations of NH₄-N, NO₃-N, NO₂-N, TN, TP and SRP were found using the linear equations from their respective standard calibration curves.

Nitrogen concentrations were determined using the phenol–hypochlorite method for NH₄⁺, N-Naphthyl-(1)-ethylenediamine-dihydrochloride for NO₂⁻ and sodium salicylate method for NO₃⁻, and Koroleff method for TN (APHA, 2005). The ammonium-nitrogen concentration was determined following the sodium salicylate method, using hypochlorite solution as a catalyst. Twenty-five (25) ml of filtered water sample was put in a 100ml conical flask, and 2.5 ml of sodium salicylate solution was added, followed immediately by the addition of 2.5 ml of Hypochlorite solution. The samples were then incubated at a temperature of 25 °C in the dark for 90 minutes, and the absorbance was read at a wavelength of 655 nm using a spectrophotometer.

The nitrite-nitrogen concentration was determined using the reaction between Sulfanilamid and N-Naphthyl-(1)-ethylenediamine-dihydrochloride. Twenty-five (25) ml of filtered water sample was put in 100ml glass conical flask and 1 ml of Sulfanilamid solution was added. After 5 minutes, 1 ml of N-Naphthyl-(1)-ethylenediamine-dihydrochloride solution was added to this mixture and gently mixed. The solution was left for 10 minutes after which its absorbance was read spectrophotometrically at a wavelength of 543 nm.

For nitrate-nitrogen, 1ml of freshly prepared sodium salicylate solution was added to 20ml of the filtered water sample. The samples were then put in the oven and evaporated to dryness at 95°C. The resulting residue was dissolved by adding 1 ml of concentrated H₂SO₄ and swirled carefully while still warm. Thereafter, 40ml of distilled water and 7 ml of potassium-sodium hydroxide-tartarate solution was added, respectively. The absorbance was read at a wavelength of 420 nm.

For total nitrogen, twenty-five (25) ml of unfiltered water sample was put in 100 ml conical flasks, and five (5) mL of potassium peroxodisulphate solution was added. The conical flasks were covered with a cotton plug and aluminium foil, and thereafter mixed carefully. The samples were then put in the oven and digested for 1 hour at 110 °C. After cooling, the contents were transferred into 50 mL volumetric flasks and mixed, and thereafter 1 mL of 1 M HCl reagent was added and mixed. The absorbance was measured at 220 and 275 nm against

distilled water as the blank. The absorbance at 275 nm was subtracted from the reading at 220 nm to obtain absorbance due to NO₃-N.

Soluble reactive phosphorous (SRP) was determined spectrophotometrically using the molybdenum blue method, with persulphate digestion prior to the molybdenum blue method for TP (APHA, 2005). For soluble reactive phosphorus, 25 ml of the filtered stream water sample was put in a 100ml glass conical flask and 2.5 ml of mixed reagent (Ammonium molybdate solution + Sulphuric acid + Ascorbic acid + Potassium-Antimonyltartrate-solution, respective rations, 2:5:2:1) was added into it. The prepared sample's absorbance was measured 15 minutes after adding reagents to the samples at a wavelength of 885 nm with distilled water as a reference.

Total phosphorus was determined by first digesting and reducing the forms of phosphorus present in the water into Soluble reactive phosphorous, using persulphate digestion Twenty-five (25ml) of the unfiltered water sample was put in a scotch bottle, and 1ml of warm $K_2S_2O_8$ solution was added. The scotch bottles were weighed without the lids and their weight noted. The lids were put back but not closed tightly after which they were autoclaved for 90 minutes at about 120°C and 1.2 atm. After cooling, the bottles were re-weighed, and the evaporated water replaced by addition of distilled water. After digestion, the total reduced forms into the SRP formed were analysed using the same procedure as for the soluble reactive phosphorus.

For total suspended solids (TSS), the concentration was estimated gravimetrically. 500ml of stream water sample was filtered through pre-weighed glass-fibre filters (Whatman GF/C, pre-dried at 95°C, 12 h). The GF/Cs were carefully folded and wrapped in aluminium foil and transported to the laboratory. In the laboratory, the GF/C filters were oven-dried (95°C) to constant weight and TSS was determined by re-weighing on an analytical balance and subtracting the filter weight. The total suspended solids was calculated out using Equation 1.

$$TSS = ((W_c - W_f) \times 10^6) V^{-1}$$
.....Equation 1 Where,

TSS = Total suspended solids (mgl^{-1}) ,

W_f = Weight of pre-combusted filter in grams,

W_c = Constant weight of filter + residue in grams,

V = Volume of water sample used in ml

3.2.3 Determination of nutrient content and maximum leaching time of the two plant species leaf litter

Leaf litter of the two most dominant riparian plant species within Kamweti River catchment based on the prevailing land use, *Eucalyptus saligna* (agricultural land use) and *Syzygium guineense* (forest) were used for this experiment (see Appendix 4 and 5, for detailed taxonomy and description on these plants). Approximately, 10 ± 1 kg of leaves (comprising of young and matured leaves) of the two riparian plant species were collected from the two land uses, air-dried at room temperature for two weeks to a constant weight before weighing.

A subsample of the previously air-dried leaves of the two plant species was sorted into three size classes (young: 1-10 cm; medium-aged: 11-15 cm, and mature: \geq 16 cm) to test whether nutrients concentrations, as well as leaching time, may vary with leaf size. For leaf nutrient content determination, *Eucalyptus* sp and *Syzygium* sp leaf litter were ground using heavy duty blender. Approximately, 20.00 ± 0.05 g of each size class was put in a 2L beaker and 1L of distilled water was added and left for 48 hours. After 48 hours of incubation, the samples were filtered using $0.45\mu m$ Whatman GF/C filters. The nutrient content of the two plant species leaf litter was determined as per APHA (2005) nutrient analytical procedures as described in subsection 3.2.2.

For the leaching experiment, approximately, 5.00 ± 0.05 g of leaf litter for each size class of the two plant species was put in a container and 1L of distilled water added. To determine the percentage mass loss as a result of leaching, triplicates leaf litter samples from each size class were retrieved after an interval of 2, 4, 6, 8,10,12 and 24 hours of incubation (Figure 3) The leaf litter were then oven-dried at 60 °C to constant mass and weighed, and thereafter combusted for 4 h at 550 °C in a muffle furnace and re-weighed (Ash Free Dry Mass = Dry Weight-Ash weight). The mass loss due to leaching over time was expressed as a percentage of original ash-free dry mass.

Exp. Time (H)	1	l-10 cr	n	1	1-15 cı	n	2	≥ 16 cm		
0	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
2	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
4	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
6	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
8	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
10	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
12	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	
24	E1	E2	E3	E1	E2	E3	E1	E2	E3	
	S1	S2	S3	S1	S2	S3	S1	S2	S3	

Figure 5:A set-up for leaching experiments using *Eucalyptus saligna* (E, shaded) and *Syzygium guineense* (S, unshaded) leaf litter in the laboratory.

3.2.4 Leaf decomposition experiment

Approximately, 5.00 ± 0.05 g of previously air-dried leaf litter of each plant species was enclosed in 10 cm by 15 cm litterbags of mesh size 0.5 mm. Before deployment, 410 litterbags were arranged into sets of five replicates (see figure 6) per plant species (2 species) in each site (4 sites) for 10 sampling occasions (400 litterbags). The 10 extra litter bags were taken to the study sites and returned to the laboratory. These litterbags were used to determine

initial ash-free dry mass (AFDM) for each species and for correction of weight loss during handling, and transportation to study sites.

The litter bags were incubated at each of the four study sites (2 forest and 2 agriculture) and secured using nylon ropes at a distance of approximately 0.2 m apart to avoid overlap and for ease of retrieval. Five replicates litter bags for each plant species leaf litter were retrieved from each site after an interval of 1, 3, 8, 14,21, 28, 35, 42, 49, and 56 days of incubation. During retrieval, a plankton net was used to enclose the litterbags to prevent loss of invertebrates and leaf fragments, and thereafter individual litterbags were put in plastic bags, preserved in 4% formalin and transported to the laboratory for analysis.

In the laboratory, the contents from each litter bag were emptied into a tray, washed into a 37 µm sieve with tap water and a fine brush to remove attached sediment, other debris, and associated macroinvertebrates. Leaf litter from the litterbags were oven-dried at 60°C to constant mass and weighed, and thereafter combusted for 4 h at 500°C in a muffle furnace (see plate 7) to determine ash weight and re-weighed to determine Ash Free Dry Mass (AFDM) as described by Benfield et *al.* (2017).

Leaf litter AFDM remaining over time was expressed as a percentage of initial AFDM (Wetzel & Likens, 1991). Initial oven-dry mass for each litterbag was converted into initial AFDM by a conversion factor estimated from extra sets of 10 litterbags. The leaf decomposition rates were estimated using the negative exponential model (Graça *et al.*, 2005) as in Equation 2.

$$W_t = W_0 e^{-k}$$
......Equation 2

Where,

 W_t = remaining AFDM at time t,

t=time (incubation days),

 W_0 = initial AFDM,

k = decomposition rate.

Macroinvertebrates found in the litterbags were removed and immediately fixed in 70% ethanol and afterwards identified to the family level under a dissecting microscope using specific identification keys according to Cummins *et al.* (2005), counted and subsequently assigned into their functional feeding groups (FFGs): predators, scrapers, collectors, or shredders (Cummins *et al.*, 2005). Macroinvertebrates data from the litterbags for each biotope per land use were expressed as abundance (number of individuals per litterbag), density

(number of individuals per AFDM remaining), taxa richness (number of taxa per litterbag) and the functional feeding groups (FFGs) namely; collectors (COL), predators (PRD), scrapers (SCR), and shredder (SHR) (Cummins *et al.*, 2005). In order to determine the source of macroinvertebrates that colonize the leaf litter in litter bags, benthos and drift were sampled as explained in sections 3.2.5 and 3.2.6.

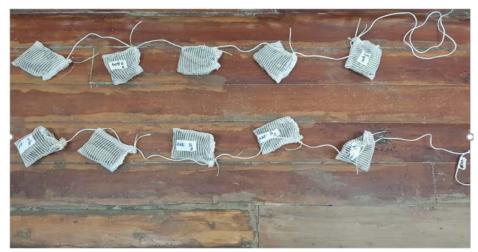


Figure 6:Leaf litter enclosed in 0.5mm, 10cm by 15cm litterbags arranged into sets of five replicates (source: This study).



Figure 7:Laboratory determination of ash weight of leaf litter using muffle furnace

3.2.5 Benthic macroinvertebrates sampling

Ten (10) benthic macroinvertebrates samples were collected during each retrieval period of the leaf litter decomposition experiment. On each sampling occasion, triplicates random quantitative samples of benthic macroinvertebrates were collected from selected sites to determine the community composition and structure using a 500 µm mesh kick net sampler, which translated to 120 benthic samples. The samples were taken by kicking the substrate for

about 30 seconds covering a sampling length of about 2 metres (see figure 8a, b). The contents of the kick net sampler were then washed into a sampling container, preserved with 4 % formalin, and transported to the laboratory for analysis. At the laboratory, the samples were washed under tap water through a series of mesh sieves (1000 µm, 500 µm and 37 µm) to remove debris, stones and wash away ethanol (Barbour *et al.*, 1999). Macroinvertebrates were sorted, enumerated and then identified to family level, and subsequently assigned into the FFGs. Macroinvertebrates in the benthic zone samples were expressed as abundance (number of individuals per m²), taxa richness (number of taxa per m²) and the four FFGs.



Figure 8(a, b): Sampling of benthic macroinvertebrates using a 0.5mm kick net sampler in agricultural (a) and forested sites (b).

3.2.6 Macroinvertebrates drift sampling

Additionally, triplicate of macroinvertebrates drift samples were collected thrice at each site in each land use during each retrieval time of the leaf litter decomposition experiment. Macroinvertebrates drift samples were collected using a 65 x 10 x 30 cm, 0.1 mm mesh drift net sampler, mounted in an upright position on a base plate, fixed to the river bottom (figure 9a, b). The drift samplers were placed facing upstream in the selected sampling sites and biotopes along the river and exposed for five minutes to capture the maximum drift density (Mureithi *et al.*, 2018).

During sampling, a velocity meter was positioned at 60% of the total water depth to measure the mean velocity over the entire water column passing through the mouth of the drift sampler. Drift samples collected in the sampler cup at the rear of the net were emptied in well-labelled sampling containers and then fixed with 4% formalin. The drift samples were taken to the laboratory, washed, and rinsed through a series of sieves (mesh size between $1000 \, \mu m$, $500 \, \mu m$ and $37 \, \mu m$) to remove ethanol and debris. The macroinvertebrates were sorted under a dissecting microscope, and then identified to the family level using keys by Cummins *et al.* (2005).

Macroinvertebrates in the drift samples were expressed as abundance (number of individuals per m³), taxa richness (number of taxa per m³) and the four FFGs as well drift densities (Individual per m³). Drift densities were determined as outlined by Bretschko (1996) by first determining the amount of filtered water (Q, m³s⁻¹) which was obtained by multiplication of the water depth, width of drift sampler and the mean velocity (m s⁻¹). To determine drift densities (individuals per m³), individual counts were divided by the total discharge.





Figure 9(a, b): Sampling of macroinvertebrate drift using a 0.1mm drift net sampler in the forested sites (a) positioning of the sampler and (b) washing the samples.

3.3 Data analysis

Descriptive statistics were used to present spatial variation in physico-chemical water quality parameters. For site characterization, the effect of land use (i.e., forest, agriculture) and streambed topography (riffle, pool) on physico-chemical variables were tested using linear mixed-effect models, with land use and streambed topography as fixed factors and land use as an interaction term with streambed topography. Principal component analysis (PCA) was

applied to summarize the variation in physico-chemical parameters and reduce data dimensionality across the land uses.

For hypothesis one, the effects plant species and leaf litter size class on leaf nutrient content was evaluated using linear mixed effect models. Similarly, for the leaching experiment, the effect of plant species, leaf litter size class and incubation time during the leaching process was evaluated using linear mixed effect models, with plant species and leaf litter size class as fixed factors fixed factors and plant species as an interaction term with leaf litter size class.

For hypothesis two, the effects of land use (i.e., forest, agriculture) and streambed topography (riffle, pool) and plant species (i.e., *Syzygium* sp and *Eucalyptus* sp) on leaf litter decomposition rate and leaf-associated macroinvertebrates were also evaluated using linear mixed-effect models, with land use, streambed topography and plant species as fixed factors and land use as an interaction term with streambed topography and plant species. The relationships between leaf litter decomposition rates, physico-chemical variables and macroinvertebrate shredders were evaluated using non-parametric Spearman's rank Correlation test (Zar, 1999).

For hypothesis three, a Non-metric multidimensional scaling (NMS; Kruskal, 1964) was applied in assessment of changes in the composition of macroinvertebrates associated with leaf litter, in drift and in the benthic zone. Bray-Curtis dissimilarity index was used to evaluate the level of dissimilarity between samples based on abundance and presence-absence data. The p-values were collected in multiple tests as described by Holm (1979) and the corrected p-values reported. Post-hoc comparisons were made using Tukey contrasts (Hothorn $et\ al.$, 2008). Models were checked for normality and homoscedasticity following Zuur $et\ al.$ (2009). Statistical analysis was undertaken using R (R Development Core Team) at a significance level of p < 0.05.

CHAPTER FOUR

RESULTS

4.1 Physico-chemical water parameters, leaching and leaf nutrient content

4.1.1 Physico-chemical variables of the two land uses

Sites in agricultural and forested land uses showed differences in physico-chemical parameters (Table 2). Agricultural sites recorded consistently higher mean values of water temperature, turbidity, electrical conductivity, total dissolved solids, total suspended solids, nitrite-nitrogen, nitrate nitrogen, Total Nitrogen and Total Phosphorous (Table 2). Pool habitat in the agricultural site recorded the highest mean temperature (18.35 \pm 0.06) while the riffle habitat at the forest site had the lowest mean temperature (14.81 \pm 0.06). A similar trend was observed with turbidity (highest = 12.12 \pm 0.33, lowest = 4.62 \pm 0.12), total phosphorous (highest =53.04 \pm 2.2, lowest =32.86 \pm 2.11), and ammonium-nitrogen (highest =29.07 \pm 2.81, lowest = 20.2 \pm 1.16) in pool(agricultural) and riffle (forest) habitats, respectively.

On the other hand, Riffle habitat in the agricultural site recorded highest mean Nitrite-Nitrogen (1.96 ± 0.33) while lowest in the riffle at the forest site (0.72 ± 0.10). A similar trend was observed with electrical conductivity (highest value= 29.78 ± 0.64 , lowest= 22.41 ± 0.51), TDS (Highest value= 15.45 ± 0.11 , lowest value= 11.89 ± 0.04), Total Nitrogen (highest value= 34.23 ± 3.73 , lowest value= 31.45 ± 3.78). Mean total suspended solids and Nitrate-nitrogen was highest at the riffles in the agricultural sites (12.52 ± 0.95 , 0.54 ± 0.01) and lowest at the pool habitat in the forest site (6.82 ± 0.48 and 0.40 ± 0.01) respectively. Surprisingly, pool habitat in the forest site recorded highest mean value of soluble reactive phosphorous (15.88 ± 1.42) while pool habitat in the agricultural site recorded the lowest mean value of soluble reactive phosphorus (7.88 ± 0.81).

Table 2: Means \pm SE of Physico-chemical water parameters measured across the study sites along Kamweti River

Parameter	Forest		Agric	ulture
•	Riffle	Pool	Riffle	Pool
Dissolved Oxygen (mg/L)	7.89 ± 0.07	7.91 ± 0.08	7.68 ± 0.08	7.58 ± 0.08
% Oxygen Saturation	97.15 ± 0.84	98.23 ± 0.89	98.69 ± 1.42	96.72 ± 0.88
Temperature (°C)	14.81 ± 0.06	15.63 ± 0.07	18.30 ± 0.06	18.35 ± 0.06
pH	6.63 - 6.83	6.72 - 6.86	6.73 - 6.89	6.78 - 6.90
Electrical Conductivity				
(µs/cm)	22.41 ± 0.51	23.12 ± 0.53	29.78 ± 0.64	29.56 ± 0.62
Total Dissolved Solids				
(mg/L)	11.89 ± 0.04	12.29 ± 0.10	15.45 ± 0.11	15.40 ± 0.07
Turbidity (NTU)	4.62 ± 0.12	5.40 ± 0.18	10.80 ± 0.27	12.12 ± 0.33
Total Suspended Solids				
(mg/L)	6.82 ± 0.63	6.82 ± 0.48	12.52 ± 0.95	11.19 ± 1.01
Soluble Reactive				
Phosphorous (µg/l)	8.65 ± 0.90	15.88 ± 1.42	10.56 ± 1.25	7.88 ± 0.81
Total Phosphorus (µg/l)	32.86 ± 2.11	44.47 ± 1.75	47.2 ± 2.17	53.04 ± 2.2
Nitrite-Nitrogen (µg/l)	0.72 ± 0.10	0.84 ± 0.15	1.96 ± 0.33	1.58 ± 0.19
Nitrate-Nitrogen (mg/l)	0.46 ± 0.01	0.40 ± 0.01	0.54 ± 0.01	0.52 ± 0.01
Ammonium-Nitrogen				
$(\mu g/l)$	20.2 ± 1.16	23.04 ± 1.88	24.91 ± 1.75	29.07 ± 2.81
Total Nitrogen (mg/L)	31.45 ± 3.78	31.93 ± 3.79	34.23 ± 3.73	33.57 ± 3.78

Both land use and streambed topography influenced physico-chemical water quality parameters (Table 3). Land use had a significant effect on dissolved oxygen, temperature, conductivity, total dissolved solids, turbidity, soluble reactive phosphorous, total phosphorous, nitrite-nitrogen, nitrate-nitrogen, ammonium-nitrogen, and total suspended solids (all p<0.05, Table 3). However, streambed topography only had a significant effect on temperature, turbidity, total phosphorous and nitrates (all p<0.05). The land use × streambed topography

interaction term was significant for temperature, total dissolved solids and soluble reactive phosphorous (all p< 0.05, Table 3).

Table 3: F and p-values for the mixed-effect models testing the effects of land use and stream topography on physico-chemical variables in the Kamweti River. Significant p values are in bold

Parameter	Land use		Topogra	phy	Land use	d use × Topography		
	$F_{1,356}$	p	$F_{1,356}$	p	$F_{1,356}$	p		
Dissolved oxygen (mg/l)	12.1	0.002	0.3	1	0.6	1		
Oxygen saturation (%)	0.0002	0.98	0.2	1	2.2	0.7		
Temperature (°C)	2398.4	0.001	47.8	0.007	36.9	0.0007		
pН	0.4	0.78	0.6	1	0.8	1		
Conductivity (µS cm ⁻¹)	142.6	0.001	0.2	1	0.6	1		
TDS	1549.1	0.001	4.2	0.2	6.9	0.04		
Turbidity	728.5	0.001	19.5	0.007	1.3	1		
SRP	7.5	0.02	4.2	0.2	20.1	0.0007		
TP	30.9	0.001	17.8	0.001	1.9	0.8		
NO_2^-	21.8	0.001	0.4	1	1.4	0.96		
NO_3 ,	105.1	0.001	17.8	0.001	5.1	0.12		
$\mathrm{NH_4}^+$	7.3	0.002	3.1	0.28	0.1	1		
TN	0.4	0.550	0.001	1	0.02	1		
TSS	40.1	0.001	0.7	1	0.7	1		

Factor 1 in the PCA ordinations explained most variation (34.5 %), distinguishing between forest and agriculture land uses (Figure 10). Steam water physico-chemical most associated with Factor 1 were water temperature, electrical conductivity, turbidity, total dissolved solids, total suspended solids, total phosphorus, nitrate, nitrite, and velocity, which increased towards agriculture. On the other hand, factor 2 was associated with dissolved oxygen, pH, and soluble reactive phosphorus. Dissolved oxygen concentration was the only variable which increased towards forest.

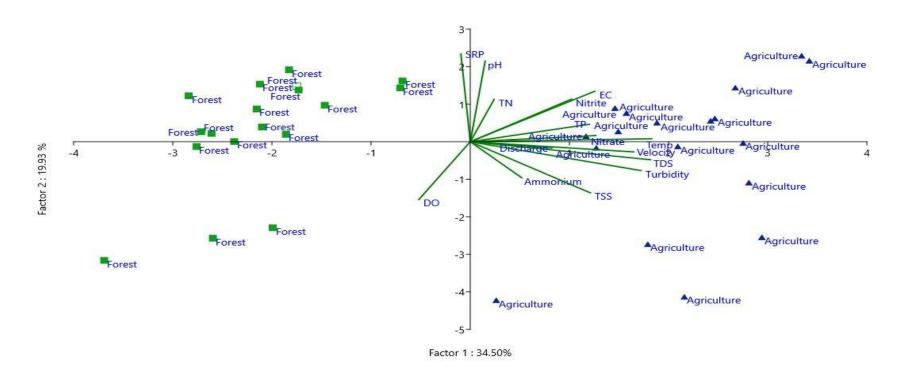


Figure 10: Principal component ordination (Components 1 and 2) of stream water physico-chemical parameters across the land uses and variation explained for each component (r^2) is expressed as a percentage.

4.1.2 Maximum leaching time for Syzygium sp and Eucalyptus sp

High rates of leaching were observed within the first six to eight hours of incubation for both *Syzygium guineense* and *Eucalyptus saligna* leaf litter (Figure 11). Thereafter, the rate decreased with time and after 12 hours of incubation, it started to level off. For *Syzygium guineense*, the young leaf litter had the lowest leaching rate at the beginning, followed by medium sized leaf litters and lastly the mature ones. After the sixth hour of incubation, the leaching rates of the young leaf litters increased drastically. On the other hand, *Eucalyptus saligna* displayed an opposite trend in terms of mass loss, where during the first six hours, the young leaf litters recorded the highest leaching rates, followed by the medium-sized and lastly the mature ones.

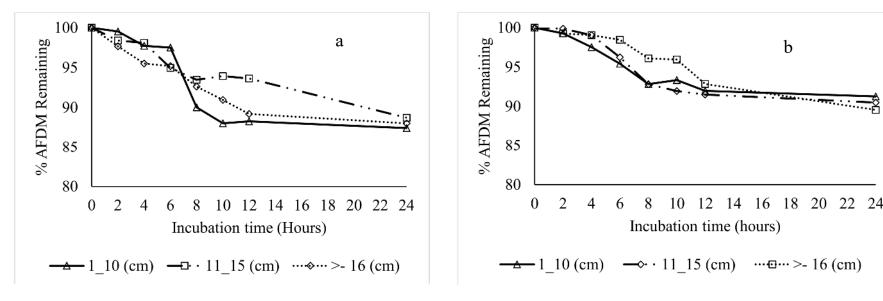


Figure 11(a, b):Percentage AFMD remaining over time due to leaching for Syzygium guineense (a) and Eucalyptus saligna (b)leaf litter.

Overall, the young leaf litter recorded the highest decomposition rates, followed by mature ones and lastly the medium-sized leaf litters (Table 4).

Table 4: Mean \pm SE of decomposition (-k/h) for Syzygium guineense and Eucalyptus saligna leaf litter

Plant Species	1-10 (cm)	11-15 (cm)	>= 16 (cm)
Syzygium guineense	0.0065 ± 0.0002	0.0048±0.0003	0.0053 ± 0.0004
Eucalyptus saligna	$0.0060\ \pm0.0001$	0.0048 ± 0.0004	0.0050 ± 0.0005

In the leaching experiment, the species of plant from which leaves were obtained had a significant effect ($F_{1,84} = 11.95$, p = 0.006) on leaf litter decomposition rate. Additionally, incubation time had a significant effect ($F_{6,84} = 3.41$, p = 0.02) on leaf litter decomposition rate. However, the size class of leaf litter did not have a significant effect ($F_{2,84} = 0.32$, p = 0.88) on leaf litter decomposition rate during leaching. Tukey contrasts indicated that there was no significant difference (t-value = 1.72, p = 0.08) between *Syzygium sp* and *Eucalyptus sp* in terms of decomposition rate during the leaching experiment. Similarly, there was no significant difference between leaf size classes (i.e., 1-10 cm, 11-15 cm, >16 cm) in terms of decomposition rate (all p>0.05). Additionally, there were no significant differences between leaf litter incubation times (i.e., 2, 4, 6, 8, 10, 12, 24 hrs) in terms of decomposition rate (all p>0.05).

4.1.3 Plant leaf litter nutrients

Leaf nutrient content differed between *Syzygium guineense* and *Eucalyptus saligna* species. *Syzygium guineense* had consistently higher concentrations of all the nutrient parameters compared with *Eucalyptus saligna*, except for total nitrogen (Table 5). This showed that *Syzygium guineense* are high quality leaf litter nutritionally compared with *Eucalyptus saligna*. It is clear that the young leaves had the highest concentration of TP and this decreased with size.

Table 5: Mean \pm SE of nutrient content for Syzygium guineense and Eucalyptus saligna leaf litter

Plant species	Size class	SRP (µg/l)	TP(μg/l)	NO ₂ -N (ug/l)	NO ₃ -N (mg/l)	NH4-N(ug/l)	TN (mg/L)
Syzygium guineense	1_10	0.55 ± 0.03	1382.38 ± 10.31	27.24 ± 2.95	7.68 ± 0.88	388.67 ± 53.67	28.76 ± 0.63
	11_15	$0.51 {\pm}~0.01$	1088.10 ± 25.43	23.81 ± 5.28	4.68 ± 1.63	421.33 ± 51.77	29.35 ± 0.55
	≥ 16	0.50 ± 0.01	1070.95 ± 13.71	18.86 ± 0.86	8.18 ± 0.25	362.67 ± 10.49	28.59 ± 0.21
	Mean	$\boldsymbol{0.52 \pm 0.01}$	1180.48 ± 51.31	23.30 ± 2.14	6.85 ± 0.77	390.89 ± 23.34	$\textbf{28.90} \pm \textbf{0.27}$
Eucalyptus saligna	1_10	0.48 ± 0.01	1155.71 ± 31.82	11.71 ± 0.29	7.22 ± 0.18	232.67 ± 2.33	29.12 ± 0.72
	11_15	0.50 ± 0.01	991.43 ± 3.30	17.05 ± 0.67	4.56 ± 1.40	215.00 ± 4.04	31.18 ± 0.49
	≥ 16	0.45 ± 0.01	766.19 ± 8.82	17.05 ± 4.27	4.40 ± 1.28	199.00 ± 1.73	32.27 ± 0.71
	Mean	$\boldsymbol{0.48 \pm 0.01}$	971.11 ± 57.26	15.27 ± 1.53	5.39 ± 0.72	215.56 ± 5.07	30.86 ± 0.56
Syzygium: Eucalyptus		1.08	1.22	1.53	1.27	1.81	0.94

The plant species from which leaf litter was obtained had a significant effect on soluble reactive phosphorous, total phosphorous, nitrites, ammonium, and total nitrogen concentrations in the leaf litter (all p<0.05, Table 6). However, the size class of leaf litter only significantly affected (p = 0.0003) the total phosphorous concentration in the leaf litter. Tukey contrasts indicated that Syzygium sp and Eucalyptus sp differed significantly in terms of soluble reactive phosphorous (t-value = 2.58, p = 0.02), total phosphorous (t-value = 11.68, p = 0.0001), nitrates (t-value = 2.45, p = 0.03), ammonium (t-value = 3.75, p = 0.002) and total nitrogen (t-value = -4.49, p = 0.0007) concentrations in leaf litter. However, in terms of leaf litter size classes, significant differences were only observed for total phosphorous concentrations between 1-10 cm and >16 cm (t-value = 14.93, p = 0.0001), between 11-15 cm and >16 cm (t-value = 8.63, p = 0.0001) and between 11-15 cm and 1-10 cm (t-value = -6.29, p = 0.0001).

Table 6: F and p-values for the mixed-effect models testing the effects of Plant species and Size class on the nutrient contents of Syzygium guineense and Eucalyptus saligna.

SRP and TN refers to soluble reactive phosphorous and total nitrogen. Significant p values are in bold.

Variable	Plant species		Size class	Size class		Plant species × Size class	
	$F_{1,12}$	p	$F_{2,12}$	P	$F_{2,12}$	p	
SRP	15.48	0.003	4.23	0.08	2.82	0.09	
Total Phosphorous	193.22	0.0003	186.21	0.0003	16.24	0.0003	
Nitrites	10.35	0.02	0.33	0.72	2.58	0.22	
Nitrates	2.67	0.24	3.41	0.18	1.72	0.244	
Ammonium	48.57	0.0003	0.82	0.92	0.39	0.92	
Total Nitrogen (mg/L)	17.16	0.003	3.97	0.08	4.13	0.08	

4.2 Leaf litter decomposition

Across land use (forest and agriculture) and streambed topography (i.e., riffles and pools), leaf litter decomposition rates were species specific, and generally displayed a similar trend, with *Eucalyptus* sp having a higher rate compared to *Syzygium* sp. Mass loss was high during the first eight days at each land uses for both plant species leaf litter (Figure 12). At the forested sites, *Eucalyptus saligna* and *Syzygium guineense* lost about 15% and 13%

respectively during their first eight days of incubation. Similarly, at the agricultural sites, *Eucalyptus saligna* and *Syzygium guineense* lost 16% and 11% respectively during the same period. At the end of the experiment (56 days of incubation), *Eucalyptus saligna* and *Syzygium guineense* lost about 93 % and 82 % respectively at the forested sites, and 83 % and 73% of the original mass, respectively, in the agricultural sites. With regard to streambed topography (i.e., riffles and pools), higher mass loss was recorded in riffles than pools across the land uses for both plant species leaf litter. Leaf litter decomposition rates were higher in forest sites than in agricultural sites as well as in riffles than in pools for both plant species, except for *Eucalyptus* sp in the riffle sites which had a higher rate in the agricultural than in the forest site (Figure 13). With regards to plant species leaf litter, mean decomposition rates were higher for *Eucalyptus* sp compared to that of *Syzygium* sp (Figure 13).

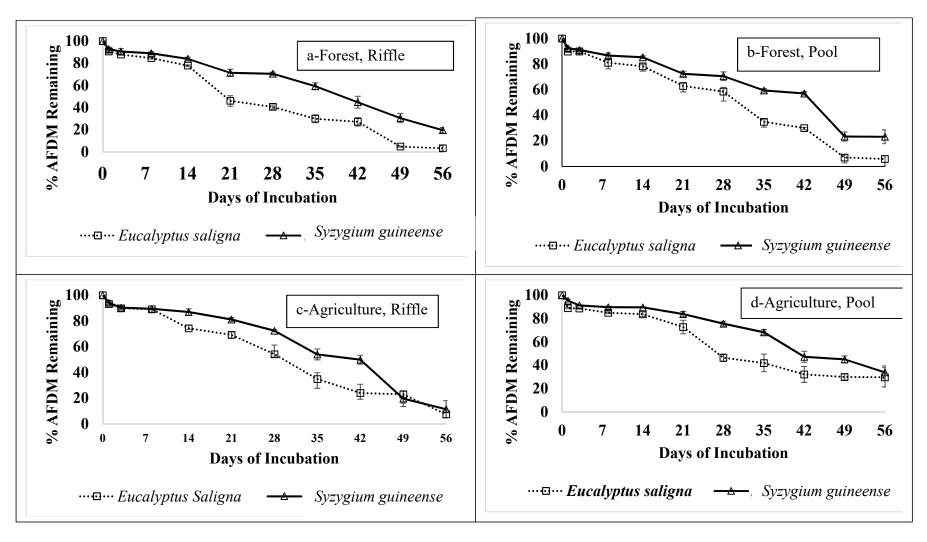


Figure 12 (a, b, c, d): Percentage AFDM remaining over time for *Syzygium guineense* and *Eucalyptus saligna* between riffles and pools across the land uses

Additionally, the biological half-life (t_{50} - time at which 50% of the original mass was processed) and t_{90} (time at which 90% of the original mass was processed) are indicated (Table 7).

Table 7: Decomposition rates of *Syzygium* sp and *Eucalyptus* sp and calculated time (days) for 50%, and 90% mass to be processed at the coefficient rate range. * indicate land use decomposition rates (*k/day*) regardless of the riffle or pool habitats.

	Streambed				
Land use	topography	Plant Species	k/day	t50(days)	t90(days)
Forest	Riffle	Syzygium sp	0.0304	23	76
		Eucalyptus sp	0.0444	16	52
	Pool	Syzygium sp	0.0234	30	98
		Eucalyptus sp	0.0371	19	62
		Syzygium sp*	0.0269	26	86
		Eucalyptus sp*	0.0408	17	56
Agriculture	Riffle	Syzygium sp	0.024	29	96
		Eucalyptus sp	0.0515	13	45
	Pool	Syzygium sp	0.017	41	135
		Eucalyptus sp	0.0233	30	99
		Syzygium sp*	0.0205	34	112
		Eucalyptus sp*	0.0269	26	86

Land use did not have a significant effect on leaf litter decomposition rates ($F_{1,384} = 0.25$, p = 1.0). However, streambed topography had a significant effect ($F_{1,384} = 6.71$, p = 0.05) on leaf litter decomposition rates. The species of plant also had a significant effect ($F_{1,384} = 33.61$, p = 0.0007) on leaf litter decomposition rates. The land use × streambed topography ($F_{1,384} = 1.45$, p = 1.0), land use × leaf species ($F_{1,384} = 0.53$, p = 1.0) and streambed topography × leaf species ($F_{1,384} = 1.01$, p = 1.0) interaction terms were not significant. Tukey contrasts indicated that leaf litter decomposition rates differed significantly (t-value = 2.20, p = 0.02) between pools and riffles. Tukey contrasts also showed that leaf litter decomposition rates differed significantly (t-values = -2.94, p = 0.003) between *Eucalyptus* sp and *Syzygium* sp. However, there was no significant difference (t-value = 0.30, p = 0.76) in leaf litter decomposition rates between forested and agricultural areas.

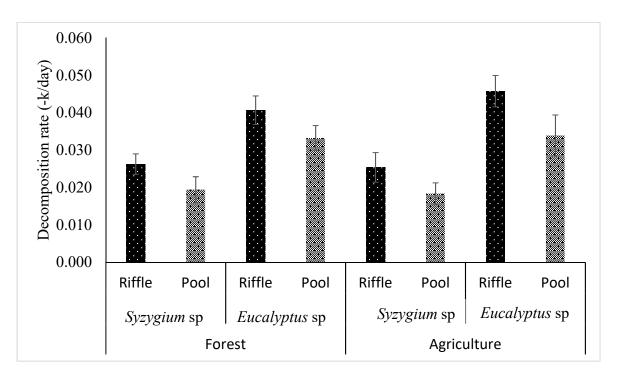


Figure 13: Mean (\pm SE) of leaf litter decomposition rate (kday-1) for *Eucalyptus saligna* and *Syzygium guineense* leaf litter across two land use (forest and agriculture) and streambed topography (Riffle and pools)

4.3 Leaf litter associated macroinvertebrates

4.3.1 Taxa composition and density of leaf litter associated macroinvertebrates

A total of 83,105 macroinvertebrates individuals belonging to 14 orders and 40 taxa (families) were found in the 400 litterbags analysed (Table 8). The structure and composition of the macroinvertebrates colonizing the leaf litters were similar, composed predominantly of members of Chironomidae, Baetidae, Lepidostomatidae, and Simulidae. Regardless of land use, streambed topography and plant species, these four taxa presented more than 85 % of the number of macroinvertebrates found. Chironomidae larvae contributed about 61.8%, while Baetidae, Lepidostomatidae and Simulidae presented 10.2 %, 7.5% and 6.0% respectively.

Mean density of leaf- associated macroinvertebrates was higher in agricultural areas compared with the forested areas, and in riffles compared with pools in both land uses. The density of leaf litter-associated macroinvertebrates was significantly influenced by land use $(F_{1,384} = 5.86, p = 0.05)$ and streambed topography $(F_{1,384} = 15.57, p = 0.0007)$. The land use × streambed topography interaction term was also significant $(F_{1,384} = 9.51, p = 0.01)$ whereas the effect of plant species on macroinvertebrates abundance was statistically insignificant $(F_{1,384} = 0.001, p = 1)$. Tukey contrasts indicated that litterbag associated macroinvertebrates differed significantly (t-value = 4.55, p = 0.0001) between pools and riffles, but not between forest and agricultural areas (t-value = 1.28, p = 0.20). Plant species did not have a significant effect on the density of leaf -associated macroinvertebrates (t-value = 1.19, p = 0.23).

The Shannon's diversity was significantly influenced by land use ($F_{1,384} = 77.18$, p = 0.0007) and streambed topography ($F_{1,384} = 16.65$, p = 0.0007). The streambed topography × leaf species interaction term was also statistically significant ($F_{1,384} = 6.09$, p = 0.05) whereas plant species leaf litter was not statistically significant ($F_{1,384} = 2.83$, p = 0.36). Tukey contrasts showed that the forested and agricultural areas (t-value = 5.61, p < 0.0001) and *Syzygium* sp and *Eucalyptus* sp (t-value = 2.73, p = 0.007) differed significantly in terms of Shannon's diversity. Riffles and pools also differed significantly (t-value = 4.23, p = 0.0001) in terms of Shannon's diversity.

Table 8. Taxa composition, abundance and richness of leaf litter associated macroinvertebrates across the land- uses. PRD(Predators), CL(Collectors), SHR(Shredders), SCR(Scrapper)

			Fo	rest	Agricu	lture
Order	Taxa	FFG	Syzygium	Eucalyptus	Syzygium	Eucalyptus
Arachnida	Araneae	PRD	3	6	6	6
Arhynchobdellida	Hirudinae	PRD	0	3	21	9
Bivalvia	Sphaeridae	CL	22	4	2	9
Coleoptera	Elmidae	SCR/SHR	195	229	45	75
	Scirtidae	SCR	466	593	469	532
	Gyrinidae	PRD	17	18	6	14
	Hydraenidae	PRD	1	0	0	0
Decapoda	Potamonautidae	SHR	48	70	88	41
Diptera	Chironomidae	CL/PRD	9598	10108	15717	15833
	Culicidae	CL	0	0	1	2
	Ceratopogonidae	PRD	136	85	132	95
	Simulidae	CL	412	487	2270	1683
	Athericidae	PRD	3	11	0	6
	Muscidae	CL	32	11	41	41
	Tipulidae	SHR	7	15	6	7
	Limonidae	SHR	1	0	2	0
	Tabanidae	PRD	2	4	7	1
Ephemeroptera	Baetidae	SCR/CL	2525	2310	1733	1705
_	Caenidae	CL	88	111	346	145
	Tricorythidae	CL	263	141	1009	565

	Prosopistomatidae	PRD	7	3	3	0
	Leptophlebidae	CL	153	134	70	94
	Oligoneuridae	CL	26	21	0	0
	Heptageniidae	SCR	194	558	163	235
	Ephemeridae		0	0	14	4
Hemiptera	Mesoveliidae	PRD	3	1	0	1
Lepidoptera	Crambidae	SHR	0	1	4	0
Odonata	Libellulidae	PRD	4	3	0	0
	Gomphidae	PRD	7	2	2	2
	Aeshnidae	PRD	10	11	3	7
	Lestidae	PRD	0	0	2	3
Oligochaeta	Lumbriculidae	CL	0	0	9	3
	Tubificidae	CL	0	1	21	40
Plecoptera	Perlidae	PRD	446	415	12	104
Trichoptera	Hydropsychidae	CL/PRD	576	469	523	386
	Leptoceridae	CL/SHR	185	125	45	17
	Lepidostomatidae	SHR	2367	2457	559	754
	Hydroptilidae		17	13	47	36
	Philopotamidae	CL	113	28	10	15
Tricladida	Planariidae	PRD	78	54	13	37
	Richness		33	34	35	34

4.3.2 Colonization patterns of Leaf litter by macroinvertebrates

Litterbags incubated at the forest areas recorded higher mean species richness compared to those at the agricultural areas. Additionally, litterbags incubated in the rifles had higher mean species richness compared with those in the pools (Figure 14). The species richness of leaf litter-associated macroinvertebrates was significantly influenced by land use ($F_{1,384} = 22.20$, p = 0.0007) and streambed topography ($F_{1,384} = 11.55$, p = 0.004). Plant species from which leaf litter was obtained did not have a significant effect ($F_{1,384} = 2.65$, p = 0.45) on the species richness of litterbag associated macroinvertebrates. Tukey contrasts indicated that forest and agricultural areas differed in terms of species richness (t-value = 3.54, p = 0.001). Tukey contrasts also showed that riffles and pools differed in terms of macroinvertebrates species richness (t-value = 3.57, p = 0.0004).

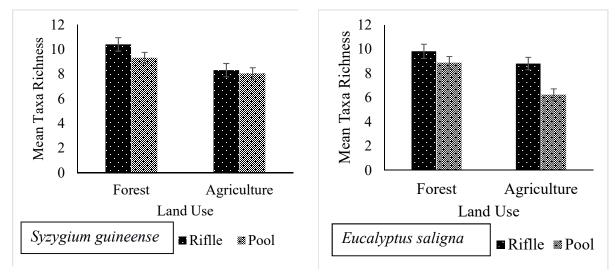
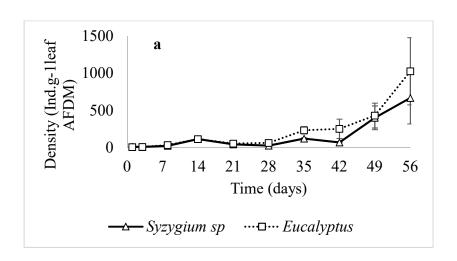
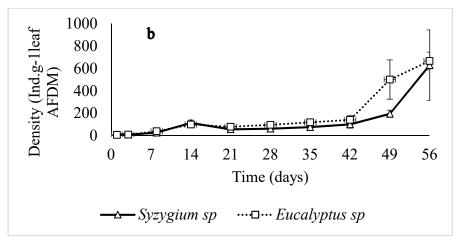
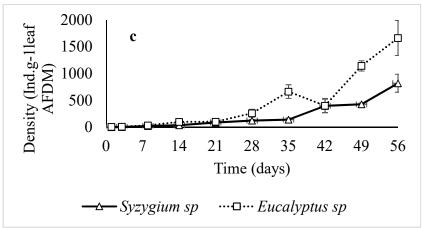


Figure 14: Mean taxa richness of leaf litter associated macroinvertebrates between riffles and pools across the land uses

Macroinvertebrates density (individuals/gAFDM) colonizing the litterbags increased with time across the land uses and streambed topography (riffles and pools), and greatest values were recorded after 56 days of incubation in both forested and agricultural sites (Figure 15a-d). Full colonization of leaf litter by macroinvertebrates was noticeable after 28 days of incubation for both plant species.







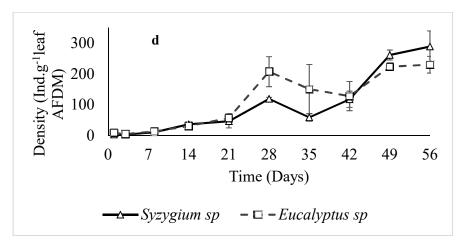


Figure 15(a, b, c, d): Mean density (Individuals/gAFDM) of leaf litter associated macroinvertebrates over time across the land uses (a: Forest-Riffle, b: Forest-Pool; c: Agriculture-riffle, and d: Agriculture-pool)

4.3.3 Comparison of drift, benthic and leaf-associated macroinvertebrates

Across the land uses, the number of taxa differed among drift, benthic and leaf litter-associated macroinvertebrates (Table 9). Highest number of taxa were recorded in benthic, followed by leaf litter associated, and lastly drift macroinvertebrates. On the other hand, highest macroinvertebrates abundance was recorded in litterbags, followed by benthic and lastly in drift. Macroinvertebrates diversity was highest in benthic, followed by leaf associated macroinvertebrates and lastly from drift. With reference to dominance, highest value was recorded for macroinvertebrates in the leaf litter associated macroinvertebrates, followed by drift and lastly benthos. Conversely, highest diversity was observed in benthic, followed by leaf litter associated macroinvertebrates and lowest in drift.

Table 9: Diversity indices among drift, benthic and leaf litter associated macroinvertebrates

	Drift	Benthic	Leaf associated
Taxa_(S)	10	52	40
Individuals	7690	10360	83105
Dominance_(D)	0.3715	0.1144	0.4023
Simpson_(1-D)	0.6285	0.8856	0.5977
Shannon_(H)	1.172	2.633	1.543
Evenness_(e^H/S)	0.3228	0.2677	0.117
Margalef	1.006	5.516	3.443
Equitability_(J)	0.5089	0.6665	0.4183

A total of 58 macroinvertebrates taxa were recorded in combined drift, benthic and litterbag samples, with 52 of this in benthic, 40 in litterbags and 10 in drift samples (Table 10) across the land uses in the study area. Only Seven taxa (12% of the total taxa) were found in drift, benthic and litterbag samples across the land use. The seven taxa include Chironomidae, Baetidae, Elmidae, Simulidae, Heptageniidae, Leptoceridae and Ceratopogonidae. Baetidae, Chironomidae and Simulidae were the major dominant taxa among the drift, benthic and leaf associated macroinvertebrates. Twenty-nine (29) taxa (50% of the total taxa) were found in both benthic and litterbag samples, while 15 taxa (25%), four taxa (7%, Culicidae, Ephemeridae, Prosopotamidae and Hydroptilidae) and two taxa (3%, Pyralidae and Hydracarina) were only recorded in the benthic, litterbags and drift macroinvertebrates respectively (Table 10). The extra two taxa (3%) were found in both drift and benthic zone.

Table 10: Taxa composition and richness in drift, benthic and leaf associated macroinvertebrates (*Syzygium* sp and *Eucalyptus* sp), + and - means presence and absence, respectively

		FOREST		AGRICULTURE				
Taxa	Benthos	Drift	Syzygium	Eucalyptus	Benthos	Drift	Syzygium	Eucalyptus
Aeshnidae	+	-	+	+	+	-	+	+
Amphizoidae	+	-	-	-	+	-	-	-
Aranaea	+	-	+	+	+	-	+	+
Athericidae	+	-	+	+	+	-	-	+
Baetidae	+	+	+	+	+	+	+	+
Belostomatidae	-	-	-	-	+	-	-	-
Caenidae	+	-	+	+	+	-	+	+
Capiteliidae	+	-	-	-	-	-	-	-
Ceratopogonidae	+	-	+	+	+	+	+	+
Chironomidae	+	+	+	+	+	+	+	+
Chrysomalidae	+	-	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	+	-	-	-
Cordullidae	+	-	-	-	-	-	-	-
Crambidae	+	-	-	+	+	-	+	-
Culicidae	-	-	-	-	-	-	+	+
Dixidae	+	-	-	-	+	-	-	-
Dolichopodidae	-	-	-	-	+	-	-	-
Elmidae	+	+	+	+	+	+	+	+
Empididae	+	-	-	-	+	-	-	-
Ephemeridae	-	-	-	-	-	-	+	+

Gerridae	-	+	-	-	+	-	-	-
Gomphidae	+	-	+	+	+	-	+	+
Gyrinidae	+	-	+	+	+	-	+	+
Helodidae	+	-	-	-	+	-	-	-
Hepatageniidae	+	+	+	+	+	+	+	+
Hirudinae	+	-	-	+	-	-	+	+
Hydraenidae	+	-	+	-	+	-	-	-
Hydracarina	-	-	-	-	-	+	-	-
Hydrophilidae	+	-	-	-	-	-	-	-
Hydroptilidae	-	-	+	+	-	-	+	+
Hydropsychidae	+	-	+	+	+	-	+	+
Lepidastoamatidae	+	-	+	+	+	-	+	+
Leptoceridae	+	+	+	+	+	-	+	+
Leptophlebidae	+	-	+	+	+	-	+	+
Lestidae	+	-	-	-	+	-	+	+
Libellulidae	+	-	+	+	+	-	-	-
Limonidae	+	-	+	-	+	-	+	-
Lumbriculidae	+	-	-	-	+	-	+	+
Mesoveliidae	+	-	+	+	-	-	-	+
Muscidae	+	-	+	+	+	-	+	+
Naucoridae	-	-	-	-	+	-	-	-
Nepidae	+	-	-	-	-	-	-	-
Oligoneuridae	+	-	+	+	+	-	-	-
Orthothrichia	-	-	-	-	+	-	-	-
Perlidae	+	-	+	+	+	-	+	+
Philapotamidae	+	-	+	+	+	-	+	+
Planariidae	-	-	+	+	+	-	+	+
Potamonautidae	+	-	+	+	+	-	+	+
Psephenidae	-	-	-	-	+	-	-	-
Prosopistomatidae	-	-	+	+	-	-	+	-
Pyralidae	-	+	-	-	-	-	-	-
Scirtidae	+	-	+	+	+	-	+	+
Simuliidae	+	+	+	+	+	+	+	+
Sphaeridae	+	-	+	+	+	-	+	+
Tabanidae	+	-	+	+	+	-	+	+
Tipulidae	+	-	+	+	+	-	+	+
Tricorythidae	+	-	+	+	+	-	+	+
Tubificidae	-	-	-	+	+	-	+	+
Richness	43	8	33	33	45	7	35	34

The overall mean proportion of macroinvertebrates taxa varied among drift, benthic and in litterbag samples (Syzygium sp and Eucalyptus sp leaf litter) across the land uses. Macroinvertebrates drift had the lowest mean proportion $(2.17 \pm 1.08, 3.22 \pm 1.41)$, in forest and agricultural sites, respectively) in both land uses. In the forested sites., benthic macroinvertebrates recorded the highest mean proportion (48.53 ± 5.70) followed by Syzygium-leaf litter associated macroinvertebrates (44.17 ± 5.64) . On the other hand, Syzygium leaf litter associated macroinvertebrates had the highest mean proportion (52.52 ± 5.41) followed by benthic macroinvertebrates (41.69 ± 5.42) in the agricultural sites. With regards to Eucalyptus sp, similar trend was observed across the land uses. Eucalyptus leaf litter-associated macroinvertebrates had the highest mean proportion $(46.00 \pm 5.30, 55.87 \pm 5.45)$, forest and agricultural sites, respectively), followed by benthic macroinvertebrates $(43.97 \pm 5.37, 38.11 \pm 5.41)$, forest and agricultural sites, respectively) and lastly macroinvertebrates drift (2.14 ± 1.06) , forest and agricultural sites, respectively).

The percentage proportion of Chironomidae in the benthos was lower than in drift and litterbag samples for both plant species across the land uses. Similarly, the percentage of Baetidae was lower in benthos than in drift and litterbag samples. Conversely, the percentage of Elmidae, Heptageniidae, Leptoceridae, Simulidae and Ceratopogonidae were lower in drift than in benthos and litterbag. On the other hand, the percentage proportion of 28 more taxa was only prominent in benthic and litterbag samples (Tables 11a, b). Furthermore, the percentage proportion of three and four other taxa was only contributed by the litterbag macroinvertebrates taxa for *Syzygium* sp and *Eucalyptus* sp respectively (Tables 11 a, b).

Table 11 (a): Percentage proportions of drift, benthic and *Syzygium* leaf litter associated macroinvertebrates

associ	Forest				Agriculture	
Taxa	Drift	Benthos	Syzygium	Drift	Benthos	Syzygium
Ceratopogonidae	0.00	32.32	67.68	16.67	10.00	73.33
Chironomidae	9.85	1.77	88.38	12.75	3.04	84.21
Elmidae	25.37	33.40	41.23	39.09	46.25	14.66
Hepatageniidae	0.85	82.85	16.30	6.21	68.48	25.31
Leptoceridae	4.27	18.38	77.35	0.00	42.31	57.69
Simuliidae	12.84	51.97	35.19	20.75	6.77	72.48
Aeshnidae	0.00	47.37	52.63	0.00	50.00	50.00
Aranaea	0.00	81.25	18.75	0.00	76.92	23.08
Athericidae	0.00	91.67	8.33	0.00	100.00	0.00
Caenidae	0.00	36.57	63.43	0.00	4.95	95.05
Crambidae	0.00	100.00	0.00	0.00	55.56	44.44
Gomphidae	0.00	72.00	28.00	0.00	50.00	50.00
Gyrinidae	0.00	37.04	62.96	0.00	64.71	35.29
Hirudinae	0.00	100.00	0.00	0.00	0.00	100.00
Hydraenidae	0.00	85.71	14.29	0.00	100.00	0.00
Hydropsychidae	0.00	39.49	60.51	0.00	50.85	49.15
Lepidastoamatidae	0.00	11.78	88.22	0.00	8.81	91.19
Leptophlebidae	0.00	32.13	67.87	0.00	38.05	61.95
Lestidae	0.00	100.00	0.00	0.00	97.70	2.30
Libellulidae	0.00	66.67	33.33	0.00	100.00	0.00
Limonidae	0.00	92.86	7.14	0.00	33.33	66.67
Lumbriculidae	0.00	100.00	0.00	0.00	18.18	81.82
Mesoveliidae	0.00	25.00	75.00	0.00	0.00	0.00
Muscidae	0.00	3.03	96.97	0.00	10.87	89.13
Oligoneuridae	0.00	91.22	8.78	0.00	100.00	0.00
Perlidae	0.00	59.08	40.92	0.00	80.00	20.00
Philapotamidae	0.00	18.12	81.88	0.00	56.52	43.48
Planariidae	0.00	0.00	100.00	0.00	13.33	86.67
Potamonautidae	0.00	80.95	19.05	0.00	59.26	40.74

Scirtidae	0.00	16.40	83.60	0.00	12.66	87.34
Sphaeridae	0.00	90.87	9.13	0.00	66.67	33.33
Tabanidae	0.00	60.00	40.00	0.00	36.36	63.64
Tipulidae	0.00	94.62	5.38	0.00	89.83	10.17
Tricorythidae	0.00	10.07	89.93	0.00	28.34	71.66
Tubificidae	0.00	0.00	0.00	0.00	22.22	77.78
Hydroptilidae	0.00	0.00	100.00	0.00	0.00	100.00
Culicidae	0.00	0.00	0.00	0.00	0.00	100.00
Prosopistomatidae	0.00	0.00	100.00	0.00	0.00	100.00
Mean Proportion	2.17	48.53	44.17	3.22	41.69	52.52

Table 12 (b): Percentage proportions of drift, benthic and *Eucalyptus* leaf litter associated macroinvertebrates

		Forest			Agriculture		
Taxa	Drift	Benthos	Eucalyptus	Drift	Benthos	Eucalyptus	
Baetidae	31.29	28.21	40.50	30.16	23.94	45.90	
Ceratopogonidae	0.00	41.29	58.71	19.74	11.84	68.42	
Chironomidae	9.41	1.69	88.90	12.67	3.02	84.30	
Elmidae	23.26	30.62	46.12	35.50	42.01	22.49	
Hepatageniidae	0.64	62.40	36.95	5.59	61.59	32.82	
Leptoceridae	5.59	24.02	70.39	0.00	63.46	36.54	
Simuliidae	11.12	45.00	43.88	25.37	8.27	66.35	
Aeshnidae	0.00	45.00	55.00	0.00	30.00	70.00	
Aranaea	0.00	68.42	31.58	0.00	76.92	23.08	
Athericidae	0.00	75.00	25.00	0.00	57.14	42.86	
Caenidae	0.00	30.43	69.57	0.00	10.78	89.22	
Crambidae	0.00	83.33	16.67	0.00	100.00	0.00	
Gomphidae	0.00	90.00	10.00	0.00	50.00	50.00	
Gyrinidae	0.00	31.25	68.75	0.00	44.00	56.00	
Hirudinae	0.00	70.00	30.00	0.00	0.00	100.00	
Hydropsychidae	0.00	38.56	61.44	0.00	56.47	43.53	
Lepidastoamatidae	0.00	11.04	88.96	0.00	6.64	93.36	
Leptophlebidae	0.00	33.33	66.67	0.00	31.39	68.61	

Lestidae	0.00	100.00	0.00	0.00	96.59	3.41
Libellulidae	0.00	72.73	27.27	0.00	100.00	0.00
Lumbriculidae	0.00	100.00	0.00	0.00	40.00	60.00
Mesoveliidae	0.00	50.00	50.00	0.00	0.00	100.00
Muscidae	0.00	7.14	92.86	0.00	10.87	89.13
Oligoneuridae	0.00	91.53	8.47	0.00	100.00	0.00
Perlidae	0.00	59.68	40.32	0.00	33.33	66.67
Philapotamidae	0.00	47.17	52.83	0.00	46.43	53.57
Planariidae	0.00	0.00	100.00	0.00	5.13	94.87
Potamonautidae	0.00	72.86	27.14	0.00	75.74	24.26
Scirtidae	0.00	12.28	87.72	0.00	10.91	89.09
Sphaeridae	0.00	98.21	1.79	0.00	30.77	69.23
Tabanidae	0.00	42.86	57.14	0.00	80.00	20.00
Tipulidae	0.00	89.13	10.87	0.00	88.33	11.67
Tricorythidae	0.00	17.58	82.42	0.00	39.43	60.57
Tubificidae	0.00	0.00	0.00	0.00	13.04	86.96
Hydroptilidae	0.00	0.00	100.00	0.00	0.00	100.00
Culicidae	0.00	0.00	0.00	0.00	0.00	100.00
Prosopistomatidae	0.00	0.00	100.00	0.00	0.00	0.00
Ephemeridae	0.00	0.00	0.00	0.00	0.00	100.00
Mean Proportion	2.14	43.97	46.00	3.40	38.11	55.87

The Non-Metric Multidimensional scaling showed that benthic macroinvertebrates were more similar in pools and riffles in the forest area than in riffles and pools in the agricultural areas. It also showed that, the macroinvertebrates in the drift, benthic and leaf litter (litter bags) were largely not similar based on abundance data (Figure 16), since it indicates a clear separation of the three macroinvertebrate group sources. The macroinvertebrates that colonized the leaf litter were similar in specific biotopes (i.e., pools) for the different plant species leaf litter across the land uses. However, based on presence-absence data, Non-Metric Multidimensional scaling ordinations indicated that benthic, and leaf litter-associated macroinvertebrates were largely similar compared to macroinvertebrates drift (Figure 17). This indicates that the difference in macroinvertebrate communities was only as a result of differences in relative abundance but not differences in taxa composition.

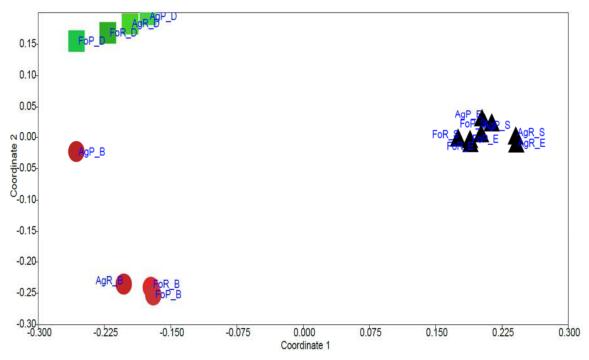
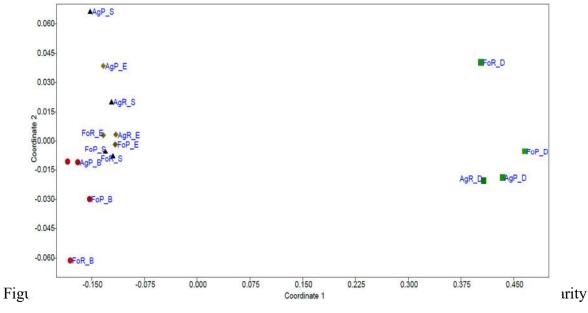


Figure 16: Non-Metric Multidimensional Scaling ordination using Bray-Curtis dissimilarity index comparing the composition of drift, benthic and leaf litter-associated macroinvertebrates based on abundance data (FoP-Forest Pool, FoR-Forest Riffle, AgP-Agriculture Pool, AgR-Agriculture Riffle, B-Benthos, D-Drift, *S-Syzygium* and *E-Eucalyptus*)



index comparing the composition of drift, benthic and leaf litter-associated macroinvertebrates based on presence-absence data (FoP-Forest Pool, FoR-Forest Riffle, AgP-Agriculture Pool, AgR-Agriculture Riffle, B-Benthos, D-Drift, S-Syzygium and E-Eucalyptus)

4.3.4 Correlation between leaf litter decomposition rates, macroinvertebrates shredders and physico-chemical water parameters

There was a weak positive correlation (r=0.07) between leaf litter decomposition rates and leaf-associated macroinvertebrates shredders abundance. There were also positive correlations between *Eucalyptus* sp leaf litter decomposition rates and ammonium (r=0.32), total nitrogen (r=0.21), velocity (r=0.03), total dissolved solids (r=0.07), turbidity (r=0.11), and temperature (r=0.002). With regards to *Syzygium* sp, there was a negative correlation between leaf litter decomposition rates and macroinvertebrates shredders (r=-0.12). However, positive correlations existed between *Syzygium* sp leaf litter decomposition rates and ammonium (r=0.16), total nitrogen (r=0.20), total suspended solids (r=0.20), and total suspended solids.

CHAPTER FIVE

DISCUSSION

5.1 Physico-chemical water parameters, leaching and leaf nutrient content

5.1.1 Physico-chemical variables of the two land uses

The stream water physico-chemical variables are influenced by both natural (i.e., rainfall intensity, river discharge, geology, topography, and vegetation cover) and anthropogenic (i.e., agriculture, abstraction, urbanisation, pollution, industrial discharges) factors over a spatio-temporal scale. Most of these anthropogenic factors form part of catchment land-use, which can have a direct effect on stream water quality (Baker, 2003). There were increased concentrations of nitrate-nitrogen, nitrite-nitrogen, total phosphorous, turbidity, total suspended solids, electrical conductivity, temperature, and velocity towards agricultural sites compared with those in the forest.

The low temperature in the forested sites could be attributed to the high canopy cover provided by intact natural riparian vegetation, which provide shading hence protecting the sites from direct solar radiation. It is reported that most native riparian trees (e.g., *Syzygium* sp) tend to grow over the stream whereas exotic tree species (e.g., *Eucalyptus* sp) are more columnar to pyramidal in shape in the agricultural sites, hence allowing much insolation. Streams that drain similar topography and geology are expected to have similar electrical conductivity. Therefore, variability of electrical conductivity in streams draining catchments of similar geology is an indication of anthropogenic activities (Masese *et al.*, 2014). Additionally, total suspended solids, turbidity and nutrient concentrations showed a relationship with land-use, however, these variables have been found to be more responsive and sensitive to local anthropogenic factors in tropical streams (Kilonzo *et al.*, 2013). This implies that variability is expected even among sites in the same catchment. Reduced canopy and riparian cover in agricultural sites due to the removal of indigenous riparian vegetation and its replacement by *Eucalyptus* sp reduces the trapping of sediment loads and incoming siltation from surface runoff, resulting in increased turbidity, total suspended solids, total dissolved solids, and nutrient concentrations.

This study reveals a significant effect of land-use on physico-chemical water parameters and its spatial effect. The evident variations in the physico-chemical parameters of water quality related to the effects of land use show that streams are extremely sensitive to environmental and land uses changes, especially in stream reaches where native riparian vegetation has been cleared to give way for agricultural activities. Previous studies have found that agricultural land use at the catchment scale is a primary predictor of water quality variables (Kirchhoff *et al.*, 2017). For instance, together with population growth, intensive agricultural

activities create a potential source of pollutants from fertilizers and sewage disposal, which often influence the hydrological system and consequently changing the surface runoff and water quality (Narany *et al.*, 2017). Additionally, Comino *et al.* (2016) demonstrated that intensive agricultural practices generate soil erosion thereby resulting to a peak of sediment discharge and increasing siltation, thus altering runoff water quality. The findings of this study indicates that the measured stream water physico-chemical parameters varied among the study sites, and most of them increased toward the agricultural sites. This shows that, the agricultural land use located downstream of the study clearly influenced the water physico-chemical parameters and hence led to the increased concentrations of nutrients, electrical conductivity, turbidity, total dissolved solids, and total suspended solids.

These findings are in agreement with previous studies research from other tropical streams (Masese *et al.*, 2014; Marmontel *et al.*, 2018), which found higher turbidity values in sites within agricultural land use and lower values in forested sites. This implies that riparian vegetation play a key role in the reduction of sediment supply from sources to stream water. The increase in turbidity concentration in the agricultural land use due to the reduction of riparian forest has also been observed in other studies in tropical agricultural microbasin which also reported higher total suspended solids in water of the stream. Furthermore, Donadio *et al.* (2005) found lower values of turbidity, total suspended solids, and total dissolved solids in sites located in the forest land-use compared to agricultural land-use in a tropical stream. This is also consistent with Gao (2008), who showed that riparian vegetation in forested headwater catchments has a significant effect on the water and sediment dynamics of rivers.

On the other hand, natural factors play a key role in the variation of water physicochemical water parameters. According to the RCC (Vannote *et al.*, 1980), the position of a stream site in its river network, measured as stream order (Strahler, 1957), is considered a surrogate of multiple environmental conditions. These conditions such as substrate composition and size, river slope, and canopy cover, can influence the water physico-chemical water parameters such as water temperature, dissolved oxygen concentrations, light penetration, turbidity and electrical conductivity (Doretto *et al.*, 2020). In particular, the RCC relates the variation of environmental parameters and energy sources along the longitudinal gradient with the trophic structure of benthic macroinvertebrates. It is predicted that the headwater streams are characterized by coarse substrates composition and a narrow width and are heavily shaded by the surrounding riparian vegetation. As a result, providing a large input of coarse particulate organic matter (CPOM) in the form of leaf litter input, low water temperature and high dissolved oxygen concentration. The influence of shading and CPOM

input by riparian vegetation decreases as stream size and width increase downstream, allowing greater light penetration into the stream and thus higher water temperature at downstream sites, which coincides with agricultural land use. Furthest downstream especially in large rivers, the influence of riparian vegetation in relation to the wetted width is nearly, resulting in higher concentrations of turbidity, total suspended solids, total dissolved solids, and electrical conductivity. In general, this means that riparian vegetation has a proven buffer capacity for preventing the transfer of diffuse contaminants to surface waters (Connolly *et al.*, 2015), making them critical for maintaining water functions and reducing eutrophication (Fernandes *et al.*, 2014; Hunke *et al.*, 2015). Thus, from the perspective of catchment management, riparian vegetation in stream channels should be encouraged, while intensive agricultural uses in adjacent areas should be avoided in order to maintain water quality (Rodrigues *et al.*, 2018).

5.1.2 Maximum leaching time for *Syzygium* sp and *Eucalyptus* sp

The findings of this study show that the patterns of mass loss due to leaching differed between *Syzygium* sp and *Eucalyptus sp*. *Syzygium* sp had higher leaching rates compared with *Eucalyptus* sp across the size classes. The decomposition rates due to leaching were higher for the young (small-sized) leaf litter compared with the medium-sized and matured leaf litter for both species. Based on Petersen and Cummins (1974), the decomposition rates for the young leaf litter was classified as medium, while that of medium-sized and mature leaf litter was classified as slow(Appendix 6).

Nykvist (1963) reported that leaching rates are species-specific, and it is related to both morphological (such as cuticle or leaf thickness) and chemical characteristics (e.g., nutrient content, concentration of tannins and lignin) of leaf litter. Therefore, the difference in leaching rates between *Syzygium guineense* and *Eucalyptus saligna* could be due to the difference in their nutrient content as shown in the results of this study, as well as their chemical and intrinsic characteristics such as leaf toughness, concentrations of tannins and lignin. According to Moore (1986), the pattern of water absorption during this first phase influences the litter leaching pattern. Therefore, the difference in water absorption patterns between these two plant species leaf litter could have also led to the difference in leaching rates of the two plant species leaf litter. On the other hand, the higher decomposition rates due to leaching for the (small-sized) leaf litter could possibly be due to the higher nutrient content such as soluble reactive phosphorus, nitrite, nitrate and total phosphorous compared to the medium-sized and matured leaf litter. Additionally, it is reported that young leaves have less accumulation of condensed

secondary metabolites such as tannins (Graça & Bärlocher, 2005) as opposed to the medium-sized and mature leaf litter hence this could have led to the increased leaching rates.

The initial phase of decomposition of leaf litter has a significant influence on subsequent processes, and the mass loss of leaf litter during this first decomposition phase has been attributed primarily to leaching (Reddy & Venkataiah, 1989). During leaching, leaf litter releases both inorganic elements such as Ca, K, Mg as well as organic compounds (Berg, 1984). Among the latter, organic acids, proteins, and soluble sugars are mainly leached at a faster rate. It has been reported that young (small-sized) leaf litter contains more soluble sugars (carbohydrates) than medium and mature leaf litter. The most abundant components of litter, cellulose, polyphenols, and lignin, decompose slowly, so high concentrations may lead to in a low decomposition rate (Swift *et al.*, 1979). These are energetic compounds that are required by microorganisms which will later decompose recalcitrant compounds like lignin and cellulose (Berg & Wessen, 1984). The result of this experiment implies that, the leaf size affect the rate of decomposition, and hence the choice of leaves during field decomposition rates should be based on the mature and senescent leaves. This is because the leaf litter that falls into the streams are mature. Otherwise, not choosing the right type of leaf size would give a wrong impression of the decomposition rates.

5.1.3 Plant leaf litter nutrient content

This study sheds new light on how leaf litter nutrient content, influence macroinvertebrates assimilation, which in turn could influence participation in the decomposition of two plant species leaf litter with contrasting characteristics. *Syzygium guineense* leaf litter recorded higher mean nutrient concentrations across the size classes compared with that of *Eucalyptus saligna*, except for TN. This indicates that *Syzygium guineense* could be more nutritional compared with *Eucalyptus saligna* leaf litter. The higher TN in *Eucalyptus saligna* does not necessarily mean that it could be better in terms of nitrogen concentration. Many ecologists consider nitrogen to be an important factor in the life histories of herbivore populations, and they have frequently attempted to link feeding to the concentration of nitrogen (N) in plants. However, this disregards the possibility that in many plants, particularly those high in tannins, animals cannot digest much of the N, and thus available nitrogen (Nitrate) concentrations may be more informative for ecologists than total N concentrations. From the results of this study, in terms of decomposition, *Eucalyptus saligna* had a higher decomposition rate than *Syzygium guineense*. This could probably show that leaf nutrients (N and P) did not play dominant roles in the decomposition of the two plant species

leaf litter in the studied stream, and instead, other factors could have led to this discrepancy. These results are in line with findings from König *et al.* (2014) who reported a negative correlation between litter decomposition rates and leaf nutrient contents. However, Roberts *et al.* (2016) reported that high N content increases the palatability and attractiveness of litter to microorganisms, resulting in greater microbial colonization that leads to higher litter decomposition rates. Similarly, Jones and Swan, (2016) found that N facilitates microbial colonization through encouraging penetration of fungal hyphae and bacterial enzymes, hence making litter more accessible to macroinvertebrates in the late stages of the decomposition processes (Jinggut & Yule, 2015).

The higher nitrogen and phosphorus content of the leaf litters in this study could be the reason for increased colonization by macroinvertebrate communities, as well as increased leaching of N (and probably other nutrients), stimulating the growth of microorganisms and thus increasing the rate of leaf decomposition rates (Mathuriau & Chauvet, 2002). Despite the difference in initial concentrations of N and P in the two plant species, it was hypothesized that all the secondary compounds were probably lost within the first four weeks of incubation as this can be supported by the full colonization pattern of leaf litter by macroinvertebrates toward the end of the experiment across the land uses in the stream.

Leaf litter decomposition is strongly influenced by the intrinsic litter characteristics. It reported that mean concentrations of N and P are the most important traits for decomposition and associated macroinvertebrate communities, followed by concentration of condensed tannins and organic carbon. There is plenty of evidence that N and P have a positive effect on decomposition (Cornelissen *et al.*, 2017). Conversely, condensed tannins are known to delay decomposition because they are resistant and toxic to microorganisms (Graça & Bärlocher ,2005). Furthermore, tannin compounds are generally inversely related to N and P (Boyero *et al.*, 2017) reinforcing differences in the quality of different litter types and hence in their decomposition. Additionally, high cellulose and lignin concentrations make leaves more rigid (Boyero *et al.*, 2012) and the polyphenols have a repellent effect toward organisms (Hepp *et al.*, 2008).

Previous studies both in the tropics and temperate regions have shown contrasting results regarding the effect of leaf quality on leaf decomposition rates. Studies by Ardon *et al.* (2009) and Li *et al.* (2009), have shown that leaf toughness is more important than N and P in controlling leaf litter decomposition rates. Another study by Pettit *et al.* (2012) observed no significance influence of lignin on mass loss despite reporting relatively high lignin content in their study species. On the contrary, lignin content had a negative impact on litter

decomposition rates, which is consistent with the findings of many other researchers who have found that a high concentration of this recalcitrant substrate inhibits decomposition in streams (Tonin *et al.*, 2014). The presence of this structural defensive compound, which confers toughness on leaf litter, protects the litter from microbial degradation and invertebrate consumption and constitutes waterproofing properties of plant cell walls, slowing down physical abrasion (Gonçalves *et al.*, 2007; Tonin *et al.*, 2014). The lignin content of leaf litter controls litter decomposition by kinetically controlling C sources for saprotrophic fungi (Gessner & Chauvet, 1994). Only specialized biota, mainly fungi, could be capable of synthesizing specialized extracellular enzymes, making lignin break down metabolically into biologically usable forms for microbes (Austin & Ballare, 2010). A study by Hepp *et al.* (2008) showed a negative relationship between polyphenols in *Eucalyptus grandis* leaf litter and macroinvertebrates and between *Eucalyptus globulus* and *Eugenia uniflora*. However, Ardón & Pringle (2008) argued that polyphenols are quickly leached in the first days of decomposition and are less important than the structural compounds in the colonization and decomposition of litter.

5.2 Land use, streambed topography and leaf litter decomposition rates

5.2.1 Land use and leaf litter decomposition rates

The main objective of this study was to assess whether the two contrasting land uses had significant effects on leaf litter decomposition rate. The decomposition rates were higher in the forested than agricultural sites and were classified as fast for both plant species based on Petersen & Cummins (1974) (Appendix 6). Additionally, the decomposition rates for both species across the land use were comparable to those found by previous researchers who worked on tropical streams (Table 12).

Table 12: Decomposition rates of plant species leaf litter recorded from previous studies carried out in the tropics. It states whether the *k* value was based upon AFDM, and coarse mesh size was used in all the cited cases

Plant Species	Location	k	AFDM?	Reference
Trema micrantha	Costa Rica	0.559	No	Irons et al. (1994)
Croton gossypifolius	Colombia	0.065	Yes	Mathuriau & Chauvet (2002)
Vanguera madagascariensis	Kenya	0.047	No	Dobson et al. (2004)
Pittosporum viridiflorum	Kenya	0.043	No	Dobson et al. (2004)
Rhus natalensis	Kenya	0.026	No	Dobson et al. (2004)
Clidemia sp.	Colombia	0.024	Yes	Mathuriau & Chauvet (2002)
Hibiscus tiliaceusa	Hawaii	0.023	No	Larned (2000)
Syzygium cordatum	Kenya	0.022	No	Dobson et al. (2004)
Dombeya goetzeni	Kenya	0.021	Yes	Mathooko et al.(2000b)
Pithecellobium longifolium	Costa Rica	0.02	No	Irons et al. (1994)
Dombeya goetzeni	Kenya	0.01	No	Dobson et al. (2004)
Psidium guajavaa	Hawaii	0.008	No	Larned (2000)
Syzygium cordatum	Kenya	0.001	Yes	Mathooko et al.(2000a)
Eucalyptus saligna	Kenya	0.039	Yes	Tsisiche et al. (2018)
Eucalyptus saligna	Kenya	0.045	Yes	Tsisiche et al. (2018)
Neuboutonia macrocalyx	Kenya	0.095	Yes	Tsisiche et al. (2018)
Neuboutonia macrocalyx	Kenya	0.062	Yes	Tsisiche et al. (2018)
Eucalyptus saligna	Kenya	0.041	Yes	This study
Eucalyptus saligna	Kenya	0.027	Yes	This study
Syzygium guineense	Kenya	0.027	Yes	This study
Syzygium guineense	Kenya	0.021	Yes	This study

The higher decomposition rates of leaf litter in forested sites compared to agricultural sites contrasts with the often-higher decomposition rates of agricultural sites in other regions (Krauss *et al.*, 2011, Martins *et al.*, 2015), where nutrient enrichment from agricultural land use can stimulate decomposition) (Allan, 2004). However, the results of this study are in agreement with Moulton *et al.* (2010) and Fugère *et al.* (2018) who found higher leaf litter decomposition rates in forested sites compared with agricultural sites. They attributed this to the low macroinvertebrates shredders abundance in the agricultural streams, leading to much

slower decomposition rates at the agricultural sites. The higher leaf litter decomposition rates in the forested compared with agricultural land use could be due to the modification of the physico-chemical water parameters and macroinvertebrate community in terms of their structure and composition. Most of the measured physico-chemical parameters (electrical conductivity, water temperature, turbidity, total suspended solids, total suspended solids, and Nitrite-nitrogen) increased towards agricultural land use but had a negative effect on the leaf litter decomposition. This could be due to increased deposition of sediment leading to burial of the most organic matter (leaf litter) and reduction in dissolved oxygen concentration thereby causing hypoxic condition. Consequently, this reduces the physical abrasion and limiting the microbial activity and macroinvertebrates colonization and assimilation (Ferreira & Chauvet, 2011), thereby negatively affecting leaf decomposition rates (Pascoal *et al.*, 2005).

The negative effect of agricultural land use on the decomposition rates of *Syzygium* sp as well as *Eucalyptus* sp, probably due to lower microbial and macroinvertebrates activity. More specifically, there was a significant difference in mean taxa richness and mean abundance of macroinvertebrates between the two land uses, with forest having higher than agricultural land use. Additionally, macroinvertebrates shredders were significantly higher in the forested sites than agricultural sites. Therefore, this could possibly be one of the reasons for the high decomposition rates in the forested sites compared with the agricultural sites. Previous research in the tropical regions, have found that streams with substantial agricultural land use in their watershed often have lower leaf litter decomposition rates than forest streams (Fugère et *al.*, 2018; Masese *et al.*, 2014; Silva-Junior *et al.*, 2014).

Agricultural land use often increases rates of microbial decomposition of leaf litter in streams because of increased water temperature and nutrient concentrations (Tank *et al.*, 2010; Young *et al.*, 2008,). Although the two agricultural sites recorded higher temperatures than the two forested sites, they also had relatively low nutrient concentrations (Fugère *et al.*, 2018), the opposite of what is usually reported (Woodward *et al.*, 2012). This could probably be due to the very low fertilizer application in the region, which leads to nutrient-depleted soils. Thus, although warmer temperatures might stimulate litter decomposition at agricultural sites, nutrient limitation might equally constrain leaf litter decomposition rates at these sites. From these results, it was concluded that, environmental factors such as nutrient concentrations can modulate and constrain decomposition rates at high temperatures (Graça *et al.*, 2015).

A large portion of the study area has been claimed entirely by monocultures of the exotic tree, *Eucalyptus saligna* plantation. Given that leaf litter produced in riparian areas is the primary energy source for small streams and that plant species differ in nutrient content,

chemical defenses, and physical attributes, Eucalyptus plantations have the potential to affect stream ecological functioning. Eucalyptus plant species produce less leaf litter than their equivalent native plant species in the forest. Similarly, it modifies the timing of leaf litter production. Because of differences in leaf composition, the nutrient input by *Eucalyptus* plant species maybe lower than the native plant species and hence affecting the stream functioning. Additionally, the low nutrient content of litter makes the decomposition rates of *Eucalyptus* plant species leaf litter to be strongly dependent on nutrients in the water. According to Graça et al. (2001), Eucalyptus afforestation might affect aquatic communities because of seasonal differences in litterfall. Additionally, the reduced litter diversity in plantations, as well as the antibiotic properties of Eucalyptus oils, may also interfere with microbial decomposition and invertebrate feeding. The finding of this study have important implications on the management of riverine ecosystems in the region. First, catchment-scale pressures can affect stream ecosystem functioning, as evidenced by the higher mean decomposition rate in forested land use versus agricultural land use. Secondly, the other importance of reach-scale influences riffle pool difference in leaf litter decomposition rates as well as in physico-chemical variables and macroinvertebrates assemblage.

5.2.2 Streambed topography and leaf litter decomposition

The higher leaf litter decomposition rates in riffle compared to pool habitats across the two land-uses indicated the importance of the differences in their physical, chemical, and biological characteristics. Riffle habitats are known to be processing zones while pool habitats are known to be retention zones (Larned et al., 2010). Water quality-related parameters (Water temperature, turbidity, total phosphorous and nitrate-nitrogen) and stream size-related parameters (velocity, discharge, and depth) showed significant differences between riffle and pool habitats. Water temperature, electrical conductivity, turbidity, total phosphorous, ammonium-nitrogen and depth were higher in the pool than in the riffle habitats. Conversely, water velocity and discharge were higher in riffle than in the pool, which is in accord with the common definitions of pools and riffles by Montgomery and Buffington (1997). Discharge, which is a function of velocity could have been attributed to the difference observed between riffle and pool habitats in terms of water velocity and depth. Therefore, this variation in characteristics between riffles and pools can modify macroinvertebrates assemblage, and consequently affect leaf litter decomposition rates. Therefore, the results of this study indicate the importance of physico-chemical water parameters as well as physical abrasion and fragmentation by the water current in the litter decomposition process.

The decomposition rate is affected by the resistance of the leaf litter as well as the velocity of the water current (Lecerf & Chauvet, 2008). In this study, the positive correlation between leaf litter decomposition and water velocity reinforced the importance of physical abrasion as among the key process stimulating the decomposition process. The differences in flow between riffle and pool habitats could have caused differences in the leaf litter decomposition rates. The findings of this study are in agreement with previous studies where relatively constant differences in decomposition rates among species under different stream conditions were reported (Webster & Benfield ,1986). Additionally, Sangiorgio *et al.* (2004) reported similar results where the same type of leaf litter displayed higher decomposition rates in lotic than in the lentic system. Thus, the higher decomposition rates in the riffles compared to pools in this study could be attributed largely to the hydrological conditions, particularly the high-current velocity and physical abrasion (Hepp *et al.*, 2008). Therefore, the increase in leaf litter decomposition rates due to these attributes suggests that changes in water flow in a lotic environment due to anthropogenic disturbance such as damming could have important ecological implications for the structure and functioning of the system (Fonseca *et al.*, 2013).

The dynamics of organic matter and inorganic nutrients have been prescribed by the stream continuum and nutrient spiralling concepts. These concepts are based on the gradient analysis popularized by Whittaker (1967), where species tend to occur within a limited range of habitats and are most abundant within their range under optimal environmental conditions. The Serial discontinuity concept (SDC, Ward & Stanford, 1983) which is associated with the RCC, refers to the longitudinal shifts of a given parameter by stream regulation. The application of SDC ranges from physical parameters (e.g., water temperature), biological phenomena at the population (e.g., species abundance pattern), community (e.g., biotic diversity) to ecosystem levels (e.g., respiration, decomposition). This concept explains the differences in microorganisms and macroinvertebrates density pattern observed between riffle and pool habitat, which in turn could affect the decomposition process.

Similarly, the nutrient spiralling concept (Newbold *et al.*, 1982), which is also an extension of the RCC, is concerned with the unidirectional and biologically mediated recycling of nutrients along the river continuum. This concept elaborates the organic matter processing along the river continuum. The unidirectional downstream flow of rivers present a dimension at spatial scale (riffles and pools) to organic matter spiralling, which is a function of both downstream transport rate and retention processes (Minshall *et al.*, 1983). A high transport rate, determined largely by high current velocity (riffles) increases the spiralling length, whereas retention and depositional mechanisms (pools, wood debris, boulders) decreases the spiralling

length. As water velocity (riffles) increases, organic matter is processed into successively smaller particle sizes (Johnson *et al.*, 1995). On the other hand, in pool habitats, and floodplains, the spiralling length may decrease, because of a high retention, both physically by sedimentation, woody debris, riparian vegetation (Pinay *et al.*, 1990).

5.3 Leaf litter associated macroinvertebrates

5.3.1 Taxa composition and mean abundance of leaf litter associated macroinvertebrates

The hypothesis for this objective was that leaf litter colonizers prefer native species (*Syzygium* sp.) to exotic species (*Eucalyptus* sp). Therefore, native species were expected to show higher decomposition rates and increased density of macroinvertebrate species. However, the mean density of the macroinvertebrates colonizing the litter was higher in the exotic plant species leaf litter compared with the native plant species leaf litter, but not significantly different. This indicates that the macroinvertebrates did not distinguish between exotic and native leaf litter, and this could be supported by the fact that the two plant species belong to the same family (Myrtaceae).

The Chironomidae and Ephemeroptera (Baetidae, Heptageniidae) taxa were the most abundant taxa of macroinvertebrates associated with leaf litter during the entire decomposition process in both the two plant species. This is consistent with research from other tropical streams (Landeiro et al., 2008; Moretti et al., 2007). According to Gonçalves et al. (2006), Chironomidae are responsible for structuring the entire macroinvertebrate community because they are disturbance-tolerant and can colonize leaf litter regardless of its quality or decomposition time. In this study, Chironomidae were able to colonize both the leaf litter, hence demonstrating their importance in aquatic systems as well as their plasticity in selecting different types of leaf litter regardless of origin, whether native or exotic. Although Syzygium sp and Eucalyptus sp showed a difference in nitrogen and phosphorus content, no significant effect was recorded on the density, and richness of aquatic macroinvertebrates. Similar results were obtained by Rezende et al. (2010) when studying decomposition rates of Hirtella glandulosa (native species) and Eucalyptus grandis (exotic species) in the same catchment in South-East Brazil. This suggests that the macroinvertebrate community is structured only by the process of ecological succession that leaf litter undergoes over time (Ligeiro et al., 2010). On the other, it indicates that the initial nutritional quality of leaf litter does not necessarily play a key role in the process of colonization by macroinvertebrates, contradicting the results found by Davies & Boulton (2009) and O'connor et al. (1991) who observed a negative effect of exotic leaf litter on macroinvertebrates, especially macroinvertebrates shredders in six subtropical Australian streams.

5.3.2 Colonization patterns of leaf associated macroinvertebrates

The mean density (Ind/gAFDM) of macroinvertebrates colonizing the leaf litter in the litterbags increased with time across the land use for both plant species leaf litter. From the result of this study, full colonization of leaf litter by macroinvertebrates began on the 28th day of field incubation and the highest mean density was recorded on the last day of incubation (56th day). Although not in the scope of this study, the increased mean density of macroinvertebrates colonizing the leaf litter in the advanced stages of decomposition indicates that colonization by macroinvertebrates correlates with leaf conditioning by the microbial community (Gessner & Dobson, 1993). These results reinforce the idea that leaf litter becomes more attractive and palatable to macroinvertebrates after microbial colonization (Gessner et al., 1999), even in tropical systems where macroinvertebrates-mediated decomposition process is said to be of minor importance (Iron et al., 1994). The results of this study corroborate with that of previous researchers working in tropical streams such as Ligeiro et al. (2010) who found higher values of macroinvertebrate richness and density at the last sampling dates and suggested that the leaf litter in the intermediate stages of decomposition presented larger quantities of resources for the associated macroinvertebrates. The high density of macroinvertebrates toward the end of the experiment could also be attributed to the continual accumulation of biofilm on the leaf litter surface (Moretti et al., 2007). The hypothesis was that macroinvertebrates colonizing decomposing leaf detritus prefer native species (Syzygium sp) rather than exotic ones (Eucalyptus sp) was not partly confirmed. However, these results are important because the native species are of good quality nutritionally compared to the exotic ones despite their lower decomposition rates. Due to their high nutrient concentration, the native plant species could act as a sieve by retaining more nutrient coming into the stream and hence, they are effective in water purification. Additionally, plant species leaf litter with low decomposition rates may be more important as substrates for the fixation of macroinvertebrates and may eventually become the source of fine particles (Ardón & Pringle, 2008). The contrasting effect of macroinvertebrates colonizing exotic and native plant species leaf litter is reinforced by the tropics' much higher riparian diversity, such that the loss or addition of one or more plant species would be less noticeable in tropical streams (Boyero et al., 2011).

In other studies, the chemical composition of the leaf litter was observed to influence macroinvertebrate colonization. This could be explained by the time it takes for each leaf litter to become more palatable and attractive to macroinvertebrates. Furthermore, it could also be an indication of the importance of microorganisms in increasing the palatability of leaf detritus for invertebrates (Graça *et al.*, 2001). Despite the higher macroinvertebrates density, in *Eucalyptus* sp compared with *Syzygium* sp, there was a weak positive correlation between leaf litter decomposition rates and macroinvertebrate shredders, and this reinforces the idea that macroinvertebrates shredders are low in tropical streams and suggest that macroinvertebrates play a minor role in the decomposition process. These results are inconsistent with previous studies (Mathuriau & Chauvet, 2002). The negative correlation found between macroinvertebrates and leaf decomposition rates, suggests that macroinvertebrates could be using the leaf litter as a substrate for attachment and feeding on particles deposited on the leaves.

5.3.3 Comparison of diversity, taxa composition and proportion of drift, benthic and leaf associated macroinvertebrates

The other hypothesis was that the macroinvertebrates colonizing the leaf litter are taxonomically similar to those from benthic and drift. This hypothesis was partly confirmed, and the results indicate that benthic macroinvertebrates were most diverse, followed by leaf litter associated and lastly macroinvertebrates drift. Despite the highest total abundance of leaf litter associated macroinvertebrates in comparison to drift and benthos, the low diversity observed was due to the high dominance of a few taxa. For example, Chironomidae contributed about 61.8%, while Baetidae, Lepidostomatidae and Simulidae presented 10.2 %, 7.5% and 6.0% respectively, totalling to about 85%. In terms of taxa composition, the macroinvertebrates colonizing the leaf litter were largely similar to those from the benthic zone. This is because about 50% of the taxa found in litterbags also occurred in the benthic samples, and only 12% of taxa were found in drift, benthic and litterbags. However, the proportion of the difference macroinvertebrates taxa among the three groups (drift, benthic and leaf-associated macroinvertebrates) differed among species. For examples, Chironomidae and Baetidae were more in drift than in benthos, and this could be concluded that, both sources contribute to the colonization of macroinvertebrates, but drift was more prominent. On the other hand, some taxa like Simulidae, Heptageniidae, Elmidae and others were more prominent in benthos than in drift and this could indicate that the benthic zone contributed more to the colonization process than drift. Moreover, a high number of taxa were only found in the benthic and litterbag sample, which could indicate that, the benthic zone could be the prominent route of macroinvertebrates colonizing the leaf litters in the litterbags. Interestingly, four taxa

(Culicidae, Ephemeridae, Prosopotamidae and Hydroptilidae) were associated only with the leaf litters, and neither in drift nor in benthic samples. These four taxa could not be accounted for as to where could be coming from, and this advocate for further long-term research. This indicates that the seven taxa that were common across drift, benthic and litterbag samples macroinvertebrates colonizing the litterbags could come from either drift or benthic zones. Chironomidae and Baetidae taxa, colonizing the litterbags came mainly from drift compared to the benthos. On the other hands, Heptageniidae, Simulidae, Leptoceridae, Elmidae and Ceratopogonidae came mainly from drift which had a higher proportion in drift than benthos. The other taxa which were only found in benthic and litterbag samples, indicate that the macroinvertebrates taxa come solely from benthic zones. Similarly, the results from the non-Metric multidimensional scaling based on presence-absence data, indicated that benthic and leaf-associated macroinvertebrates taxa were largely similar to benthic zone but different from drift.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

- (i) Syzygium guineense leaf litter had a higher nutritional quality than Eucalyptus saligna
- (ii) The maximum leaching time for both plant species leaf litter was established to be 12 hours. Small-sized (young) leaf litter have higher decomposition rates due to leaching compared with medium-sized and mature leaf litter.
- (iii) Streambed topography had a significant effect on the decomposition of leaf litter than land use, hence local scale factors are more important in the decomposition process than catchment scale factors.
- (iv) Leaf litter associated macroinvertebrates were largely more similar taxonomically to benthic than to macroinvertebrates drift.

6.2 Recommendations

- (i) Eucalyptus saligna contributes leaf litter of lower nutritive value hence its afforestation along the riparian zones should be discouraged.
- (ii) The choice of leaf litter for the decomposition experiment should be based on size, and mature leaves should be used.
- (iii) Conservation and management efforts should be directed to the local scale factor as opposed to only riparian and catchment factors.
- (iv) A long-term study should be done to account for the other leaf-litter associated macroinvertebrates species that were neither found in benthic nor in drift.

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APPENDICES

Appendix 1: Classes for habitat quality assessment

Table 13:Classes for assessment of habitat integrity (Kleyhanns, 1996)

CLASS	DESCRIPTION	SCORE (% OF TOTAL)	
Α	Unmodified, natural.	100	
В	Largely natural with few modifications. A small change from natural in habitats and biotas may have taken place, but the ecosystem functions are essentially unchanged.	80-99	
С	Moderately modified. A loss of and change from natural habitats and biotas has occurred, but the basic ecosystem functions are still predominantly unchanged.		
D	Largely modified. A large loss of natural habitats, biotas and basic ecosystem functions has occurred.	40-59	
E	The losses of natural habitats, biotas and basic ecosystem functions are extensive.		
F	Modifications have reached a critical level and the lotic system has been completely modified, with an almost complete loss of natural habitats and biotas. In the worst instances, basic ecosystem functions have been destroyed and the changes are irreversible.		

Appendix 2: Lambert-Beer law of concentration verses Absorbance

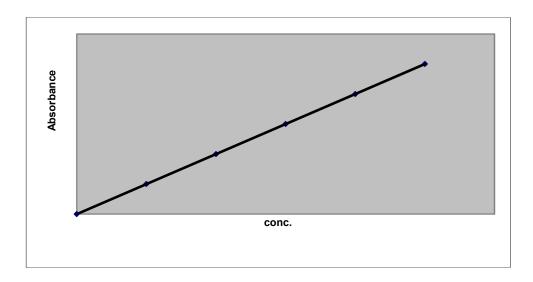


Figure 18:Standard curve for determination of formula relating absorbance to concentration.

Appendix 3:Taxonomy and description of Syzygium guineense

Syzygium guineense is a plant species of the family Myrtaceae, native to the wooded savannah and tropical forests of Africa (Orwa et al., 2009). The name genus Syzygium is derived from the Greek word 'syzygios' which means 'paired', because of the leaves and twigs that grow at the same point in several species. The specific name guineense is derived from 'Guinea', where the tree was first collected and described (Orwa et al., 2009). It's commonly referred to as 'water pear' on account of its preference for stream banks and to its wood, supposedly like that of a pear.

It is a medium-sized evergreen tree, 15-30 m high (Orwa *et al.*, 2009). The bark varies in subspecies and is greyish-white and smooth in young trees, and turn rough, creamy, and dark brown in mature trees. *Syzygium guineense* have thick and angular stem, with bundles of fibrous aerial roots. The leaves are simple and elliptic with untoothed and slightly rolling inward and narrow margins at both ends. Its average leaf length varies between 5-17.5 cm, and width of 1.3-7.5 cm. *Syzygium guineense* flowers twice in year in an area with two rainy seasons, during the short dry season and towards the end of the long rains. However, it flowers once areas with one rainy season, especially towards the end of the dry season and extending into the rainy season. *Syzygium guineense* usually occurs in lowland rain forests, mountain rain forests, fringing riverian swampy forests and open woodland. It usually grows in moist conditions, sometimes even in water, and is usually found along streams and on rocky ground in high rainfall savannah. It can grow in an area with an altitude of between 0-2100 m, mean annual temperature of 10-30°C and a mean annual rainfall of 1 000-2 300 mm.





Figure 19:Syzygium guineense leaf litter sample

Appendix 4: Taxonomy and description of Eucalyptus saligna

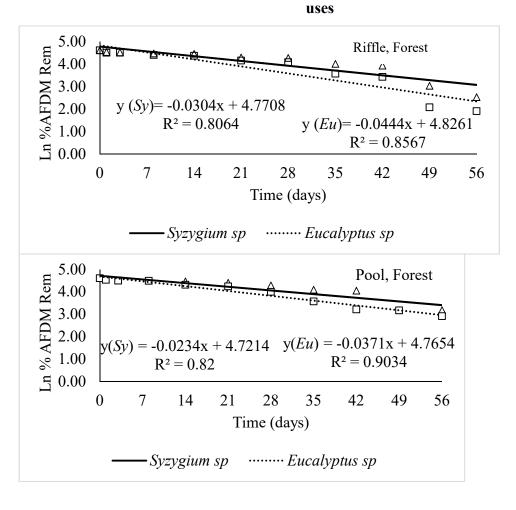
Eucalyptus saligna, which is commonly known as "Sydney blue gum" (Ritter, 2014), of the family Myrtaceae (where Syzygium sp are also belongs), is a large and tall tree, which can grow to a height of between 30 to 60 meters tall. Eucalyptus saligna was first formally described in 1797 by James Edward Smith. The leaves are petiolate, about 9–19 cm long and 1.8–3.5 cm wide and they are falcate in shape, with acuminate apex and prominent reticulate veins (Flores et al., 2016). They also have a unilayered epidermis with cells varying from tabular to round shapes and covered with a thick cuticle.





Figure 20: Eucalyptus saligna leaf litter sample

Appendix 5:AFDM remaining over time and decomposition rates per day (slope) for *Syzygium guineense* and *Eucalyptus saligna* between riffles and pools across the land



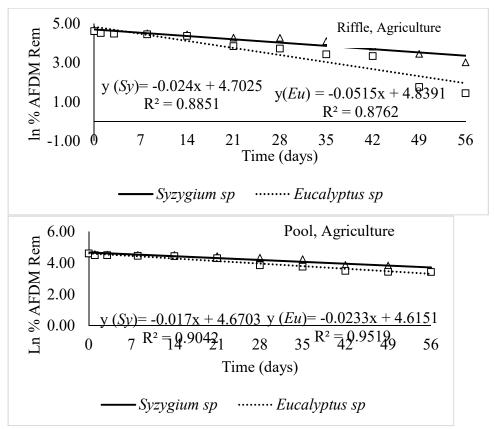


Figure 21:Natural logarithm of percentage AFDM remaining over time and decomposition rates per day (slope) for *Syzygium guineense* and *Eucalyptus saligna* between riffles and pools across the land uses (Sy refers to *Syzygium guineense* and Eu refers to *Eucalyptus saligna*).

Appendix 6: Categories of decomposition rates

Table 14: Categories of decomposition rates (k) and calculated time (days) for 50%, and 90% mass to be processed at the coefficient rate range based on Petersen and Cummins (1974).

Category	k	$t_{50} (0.693/k)$	t ₉₀ (2.303/k)
Group I (Fast)	>0.010	<46	<230
Group II (Medium)	0.005-0.010	46-138	230-461
Group III (Slow)	< 0.005	>138	>461

Appendix 7:Macroinvertebrates drift metrics

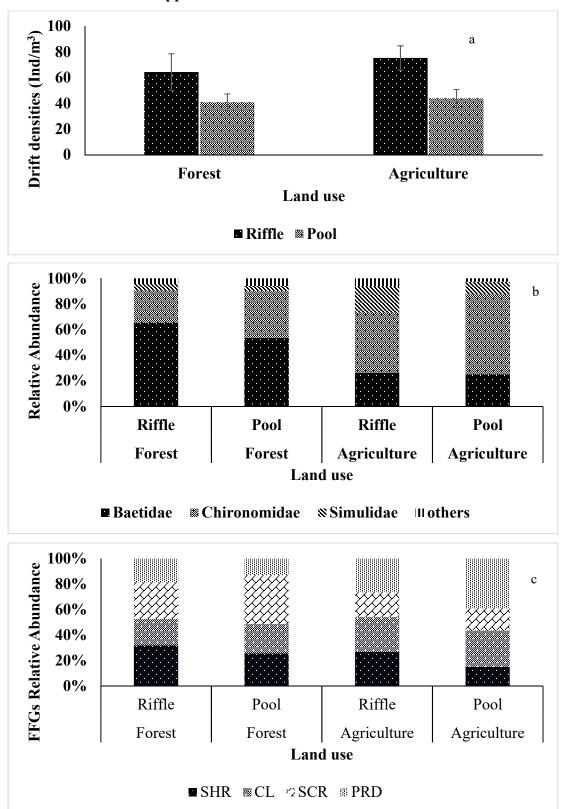


Figure 22:Macroinvertebrates (a) drift density, (b) relative abundance of most dominant taxa, and (c) FFGs

Appendix 8:Benthic macroinvertebrates metrics

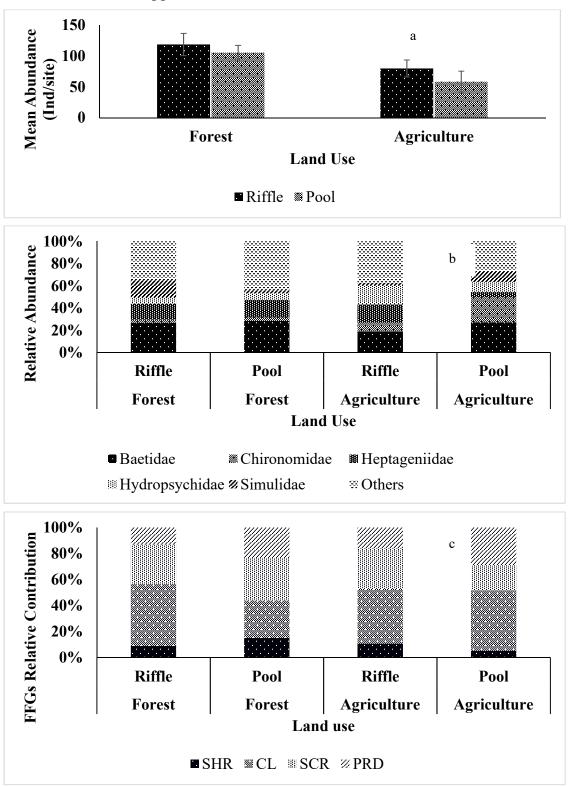


Figure 23:Benthic macroinvertebrates (a) abundance, (b) relative abundance of most dominant taxa, and (c) FFGs.

Appendix 9:Leaf-associated macroinvertebrates (a-Syzygium sp), (b-Eucalyptus sp) and (c-FFGs)

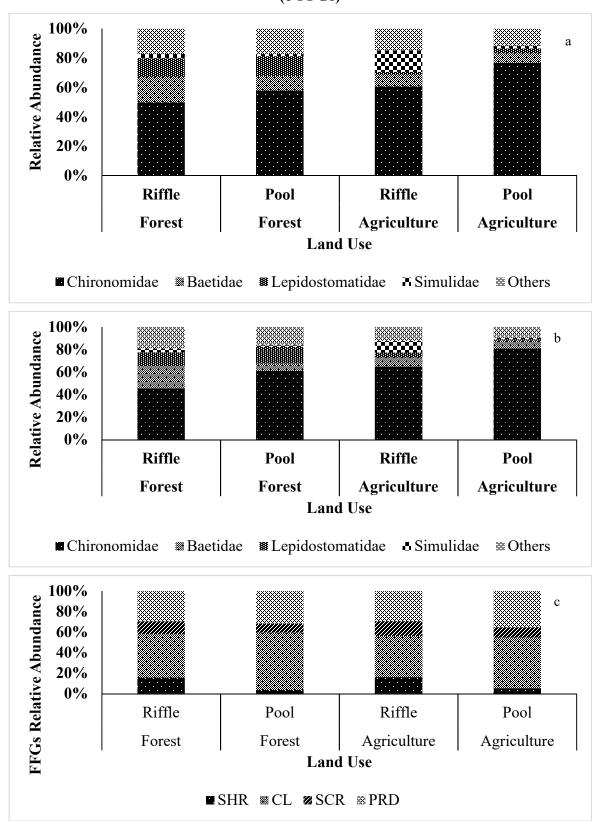


Figure 24:Relative abundance of the most dominant Leaf-associated macroinvertebrates (a-Syzygium sp), (b-Eucalyptus sp) and (c-FFGs)

Appendix 10:Leaf-associated macroinvertebrates metrics

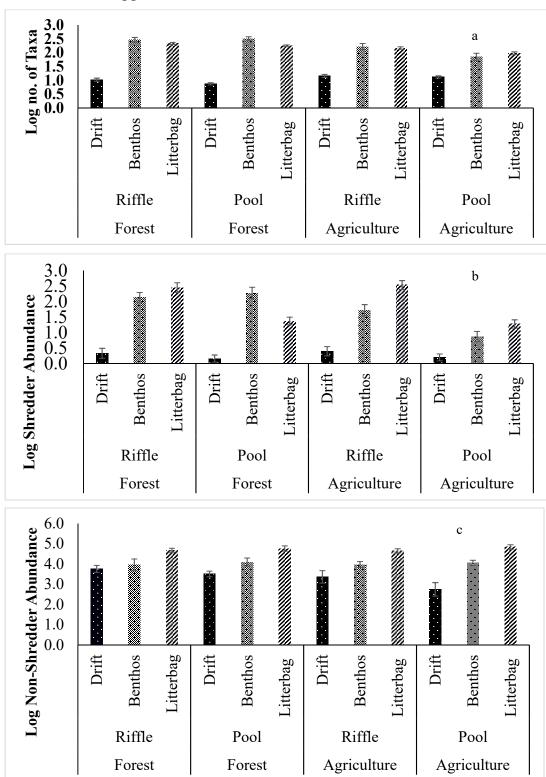
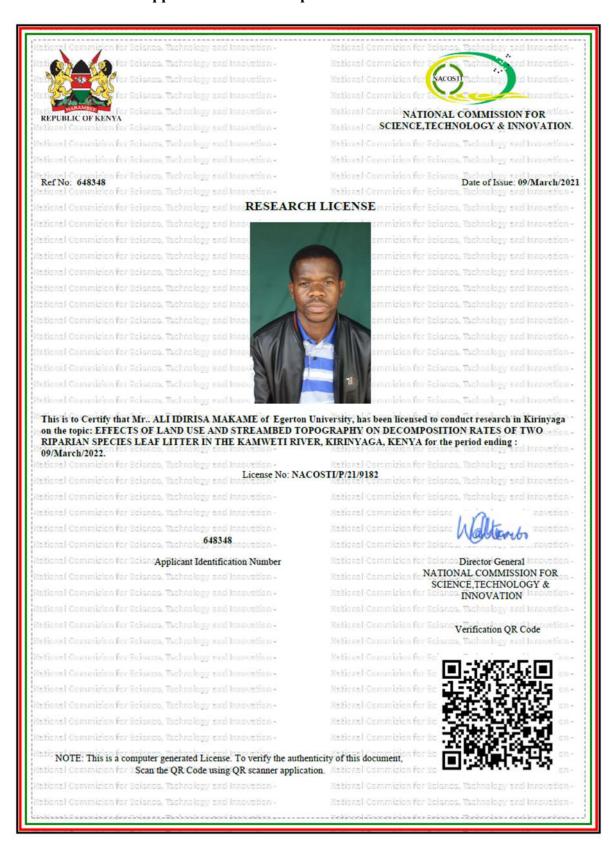


Figure 25: Log number of taxa, log number of shredder abundance and log number of non-shredder drift, benthic and Leaf-associated macroinvertebrates (a-log number of taxa), (b-log shredder abundance and (c-log non-shredder abundance)

Appendix 11:Research permit from NACOSTI



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