

Longitudinal vegetation turnover in an eastern Rift Valley riparian corridor

Giulia Silvia Giberti^{1,2} | Bruna Gumiero¹ | Alfred Koech Kiprotich³ |
Stephen Wanjiku Methu³ | David Malcolm Harper^{3,4,5} | Nic Pacini^{3,4,6} 

¹Department of Biological, Geological and Environmental Sciences, University of Bologna, Bologna, Italy

²Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy

³Naivasha Basin Sustainability Initiative, Karagita, Kenya

⁴School of Geography, Geology and the Environment, University of Leicester, Leicester, UK

⁵Freshwater Biological Association, Ambleside, Cumbria, UK

⁶Department of Environmental Engineering, University of Calabria, Arcavacata di Rende, Italy

Correspondence

Nic Pacini, Department of Environmental Engineering, University of Calabria, Arcavacata di Rende, 87036, Italy.
Email: nic.pacini@unical.it

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Abstract

East African riparian corridors are biodiversity hot spots that occur in catchments degrading under deforestation and overgrazing. Quadrats and belt transects were employed to investigate plant succession along the River Gilgil, in the Kenyan Rift Valley. The study found that most species (total 365) were broadly distributed across the tropics, but Rift Valley endemics were 12.5%, and 4%–18% were exotic. Plant composition varied with altitude, lithology, soils and rainfall. Agglomerative (Jaccard) hierarchical clustering and Non-metric Dimensional Scaling identified two and three vegetation groups, for quadrats and transects, respectively, correlated with lithology and soils. Indicator species analysis highlighted that the upstream portion of the catchment was characterised by forest taxa with few exotics. The downstream included woodland species adapted to mesic/xeric conditions and to overgrazing. Longitudinal change in species composition (β diversity) between sites was assessed by taking into consideration the contribution of 'spatial species turnover' and 'nestedness', resulting from species replacement and species loss, respectively. The β diversity of the riparian corridor vegetation was 0.40 and spatial turnover accounted for 80%–85% of this, while the rest was attributed to the nestedness component. Riverine and native trees increased downstream but with low regeneration. Afromontane vegetation extended its distribution towards lower altitudes. **Keywords** Afromontane vegetation, floodplain degradation, introduced species, Naivasha Basin, β diversity

Résumé

Les corridors riverains d'Afrique de l'Est sont des hauts lieux de la biodiversité qui se trouvent au sein de bassins versants en déclin sous l'effet de la déforestation et du surpâturage. Des quadrats et des transects en bande ont été utilisés afin d'étudier la succession végétale le long de la rivière Gilgil, dans la vallée du Rift au Kenya. L'étude a révélé que la plupart des espèces (365 au total) étaient largement réparties au sein des régions tropicales. Cependant, les espèces endémiques de la vallée du Rift représentaient 12,5 % d'entre elles, et 4 à 18 % de ces mêmes espèces étaient exotiques. La

composition végétale variait selon l'altitude, la lithologie, les sols et les précipitations. Le regroupement aggloméré hiérarchique (Jaccard) et la mise à l'échelle dimensionnelle non métrique ont permis d'identifier deux et trois groupes de végétation, pour les quadrats et les transects respectivement, en corrélation avec la lithologie et les sols. L'analyse des espèces indicatrices a mis en évidence que la partie en amont du bassin versant était caractérisée par des taxons forestiers comprenant peu d'espèces exotiques. La partie en aval comprenait des espèces forestières adaptées aux conditions mésiques ou xériques et au surpâturage. Le changement longitudinal de la composition des espèces (diversité β) entre les sites a été évalué en tenant compte de l'influence de la « rotation spatiale des espèces » et de l'« imbrication », résultant respectivement du remplacement et de la perte d'espèces. La diversité β de la végétation du corridor riverain était de 0,40 et la rotation spatiale représentait 80 à 85 % de cette même diversité, tandis que le reste était attribué à l'imbrication. L'abondance d'arbres riverains et autochtones a augmenté en aval. Toutefois, leur degré de régénération était faible. La répartition de la végétation afromontagnarde s'est étendue vers les basses altitudes.

1 | INTRODUCTION

Riparian corridors are ecotones between adjacent aquatic and terrestrial ecosystems. Their high species richness (α diversity) is under the influence of multiscale controls (Sarr & Hibbs, 2007), resulting in a combination of specialised riverine taxa as well as up-valley taxa that penetrate riparian zones by taking advantage of favourable microclimatic conditions developing along riverbanks. In the tropics, the species gradient between streams and up-valley is particularly steep (Sabo et al., 2005). High rates of species turnover (β diversity) between adjacent biotopes are achieved within extremely small spatial scales (Sabo & Soykan, 2006). Species turnover also tends to be high along streams, under the influence of the altitudinal distribution of rainfall and temperature, as well as because of longitudinal changes in geological background (Nucci et al., 2012).

Riparian vegetation structure supports important ecological functions by regulating temperature regimes (Garner et al., 2017; Trimmel et al., 2018), retaining sediments and nutrients (Boz & Gumiero, 2016; Gumiero & Boz, 2017), regulating their availability in adjacent biotopes (Naiman et al., 1993), stabilising banks (Sabater et al., 2003; Sweeney et al., 2004), diversifying habitats for other species, providing refuge during drought and preferential dispersal routes. Compositional diversity and functional diversity are strongly correlated to the ability of riparian corridors to provide multiple ecosystem services (Grizzetti et al., 2016; Naiman et al., 1993; Vidal-Abarca Gutiérrez & Suárez Alonso, 2013). Patterns of riparian corridor biodiversity are important research objectives for setting conservation priorities within globally recognised biodiversity hot spots. Our study area is in the Eastern Arc Mountains, part of the Eastern Afromontane Biodiversity hot spot, globally important for

species conservation (Critical Ecosystem Partnership Fund, 2012; Mittermeier et al., 2005).

The presence of riparian corridors significantly increases regional species lists, particularly in East African river basins that are undergoing significant hydrological changes (Guzha et al., 2018). Replacement of the pristine vegetation along the Rift Valley slopes with crops and tree plantations causes loss of biotic integrity and makes local climate warmer after deforestation (Hesslerová & Pokorný, 2011). Extensive logging and farming have severely affected forests outside protected areas and gazetted forests managed by the Kenya Forestry Service, and riparian corridors are often the only remaining forested portions within a highly fragmented landscape (Enanga et al., 2011; Everard et al., 2002; Lelo et al., 2005; Mathooko et al., 2009; Shivoga et al., 2007).

Despite their relevance in terms of the enhancement of catchment biodiversity and ecosystem services, the vegetation of stream corridors draining the Rift escarpment is poorly studied. Descriptions were made of East African lowland floodplains (Hughes, 1990; Medley, 1992), while the highland stream corridors received little scientific attention (Mathooko & Kariuki, 2000). The present study focussed on the riparian plant community of a small stream representing typical features that characterise running waters draining the central Kenyan Rift Valley. We analysed longitudinal species turnover, highlighting patterns related to climate, geological background, soils and anthropogenic influence. Community composition was assessed in terms of species origin and preferred habitat. We seek to establish whether the riparian corridor community is coherent with the potential vegetation of the surrounding landscape or forms a community characterised by specialised taxa, whose presence may dominate patterns of longitudinal β diversity change.

2 | METHODS

2.1 | Study area

Equatorial Kenya is characterised by monsoonal climate with two rainy seasons (March–May and October–December; Lamb et al., 2003). The Gilgil River originates from the confluence of two tributaries that stem from springs in the Bahati Highlands, just below the Equator. Starting from the springs, the river system flows southwards for 58 km before entering Lake Naivasha at 1889 m a.s.l. (Figure 1). The springs at approximately 2750 m a.s.l., above Gwakiongo Dam (Mirangine location), receive average annual rainfall of ca. 1300 mm (Kibona, 2000), while at the river mouth, the average rainfall reaches only ca. 610 mm year⁻¹ (Lamb et al., 2003) and average annual temperature is ca. 17°C (Odongo et al., 2016). The basin covers about 402 km², and annual average flow is 24×10^6 m³ per year (Everard et al., 2002). The upper catchment is cool and well-watered, but it becomes semi-arid below Gilgil Town (2010 m a.s.l.). The lower portion of the catchment is characterised by high incident radiation and an annual mean potential evaporation, which on average corresponds to the double of average precipitation (Odongo et al., 2015). At the peak of the dry season, the stream may remain dry for many days; the frequency of such events has been increasing during the last 20 years (D.M. Harper, N. Pacini, personal observation).

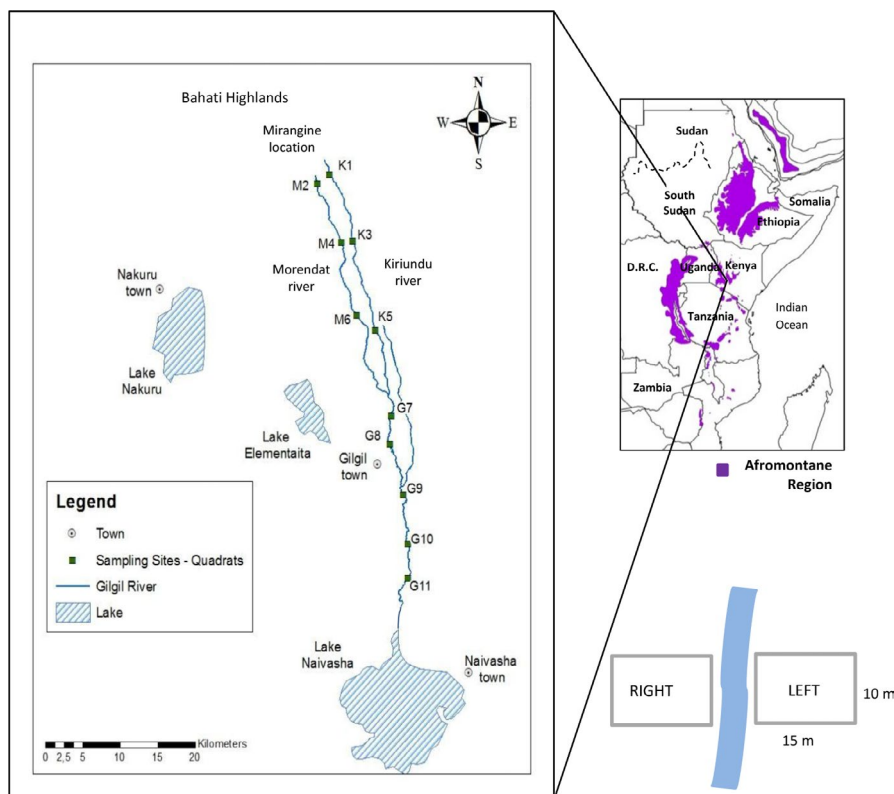
The upper and lower portions of the catchment differ in both geology and climate. The Bahati escarpment consists of Tertiary to Quaternary (Pliocene) basalt and other igneous rocks (Saemundsson, 2008), overlain by deep and fertile volcanic nitisols. The valley floor

is underlain by the Pre-Cambrian Basement complex, consisting of weathered gneisses, schists and granulites covered by Quaternary volcanic deposits. The area to the North of Lake Naivasha is covered by lacustrine sediments deposited during the Pleistocene, when present-day lakes Naivasha, Elementaita and Nakuru used to form a single basin (Richardson & Richardson, 1972).

The upper catchment is narrow with two deeply cutting tributaries: the Kiriundu (formerly “Karindo”) and the Morendat (formerly “Oleobar”), flowing between steep slopes in several sections that are inaccessible to grazing mammals. The riverbed has a step-pool morphology with frequent cascades. In the lower catchment, the floodplain broadens while the river channel alternates between short riffles and long glides deeply incised in alluvial deposits. The flow experiences wide seasonal variations, but with little overbank flooding.

Livestock watering, damming, wetland drainage, charcoal burning, littering and water abstraction are widespread in the upper catchment. Alien tree plantations (*Acacia mearnsii* De Wild., *Eucalyptus globulus* Labill. and *Hesperocyparis lusitanica* (Mill.) Bartel) and cultivated plots (cabbage, kale, potatoes and maize) extend sometimes up to the riverbank, causing corridor fragmentation. Daily collection of water, and cattle watering and washing are common. The Gwakiongo Dam (ca. 2.5 km²) receives drainage from the wetlands just below the source of the Morendat, while many other minor dams occur in the upper part of the catchment. The second largest dam is at Gilgil Town. The section downstream, below Gilgil Town, is characterised by several watering points and fords, where cattle trampling degrades the vegetation cover and interrupts the

FIGURE 1 Location of vegetation quadrat sites along the Gilgil River and tributaries (Morendat and Kiriundu). On the right: a diagram representing the positioning of right and left quadrats in correspondence of each site



continuity of the stream corridor. This lower portion of the sub-catchment has lower human population density, with few roads and little infrastructure. Signs of floodplain degradation are common, with significant corridor narrowing, channel incision and severely eroded banks.

A *Potential Natural Vegetation map of Eastern Africa* was developed under the project *Vegetation and climate change in Eastern Africa* (VECEA project, van Breugel et al., 2015). A detailed documentation on the species composition of potential vegetation types is provided in a sister publication (Kindt et al., 2015). According to the VECEA Project maps, the study area above the sources is classified under the potential 'Afromontane bamboo (B)' vegetation group. Just below the sources, the upper catchment is classified as 'Afromontane undifferentiated forest (Fb)'. The lower section of the catchment corresponds to VECEA category 'Evergreen and semi-evergreen bushland and thicket (Be)'. This formation typically degrades into 'Upland *Acacia* wooded grassland (We)' and '*Acacia-Commiphora* deciduous wooded grassland (Wd)' as a consequence of grazing and fire (Kindt et al., 2011), which are common in our lower catchment. This area receives no reliable rainfall and is used for cattle and game ranching (Jaetzold et al., 2006). The lowest site, situated above the confluence with Lake Naivasha, is within the area classified as VECEA's 'Riverine wooded vegetation (R)'.

The catchment is in Gilgil location (Nakuru County), with a mean population density of 178 inhabitants km⁻²; the only urban centre is Gilgil Town, with 60,000 inhabitants (Kenya National Bureau of Statistics, 2020).

2.2 | Gilgil sub-catchment land-use classification

A land-use map was created in ArcGIS 10.4 by visual interpretation of Google Earth Pro high spatial resolution imagery taken in April 2017 (Google Earth, 2019). According to the imagery patterns, the following categories were created as follows:

- Dark green patches with visible crown tree layer were assigned to the 'Forest' category;
- Pale green patches with a visible crown tree layer were assigned to 'Bushland';
- Pale brown background with scattered trees was assigned to 'Dry wooded grassland';
- Large farming plots (>0.14 km²) arranged in distinct geometric shape (e.g. circular) were assigned to 'Intensive agricultural farmland';
- Landscape interspersed with small scale plots was assigned to 'Extensive agricultural farmland';
- Urbanised areas, roads and infrastructure, visible in white colour, were assigned to 'Settlements';
- Water bodies were assigned to 'Lake' (which comprised also the Gwakiongo Dam);
- Dark green and flat surfaces in the proximity of the river mouth were assigned to 'Wetlands'.

The distinction between the above-mentioned categories was confirmed by visual assessment during field activities. These categories were compared with the potential vegetation mapped by the VECEA project (van Breugel et al., 2015), to assess the extent of land-use change.

2.3 | Sampling design

We used a combination of two strategies: quadrats and transects, to take into account the fact that riparian plant diversity is under the influence of processes acting at multiple spatial scales (Nucci et al., 2012; Sarr & Hibbs, 2007). An initial vegetation survey took place between December 2017 and January 2018 in 11 sampling sites distributed along the main three reaches of the Gilgil sub-catchment (three on the Morendat reach, three on the Kiriundu reach and five on the Gilgil main river reach; Figure 1). Following preliminary field visits and an assessment of Google Earth imagery, the location of each site was determined according to ease of access and avoidance of degraded vegetation, settlements and cultivated plots. At each site, we placed a 10 × 15 m quadrat on each bank, stretching from the river edge to include a 15-m wide vegetation strip (Figure 1). In order to accurately record all the above-ground vegetation, the assessment proceeded by considering first the herbaceous layer (<0.3 m height), then shrubs (0.3–1 m) and finally trees (>1 m). Each quadrat was subdivided into 3 (5 m wide and 10 m long) strips, analysed one after the other. Taxa that could not be identified in the field were photographed, and samples were collected for later processing.

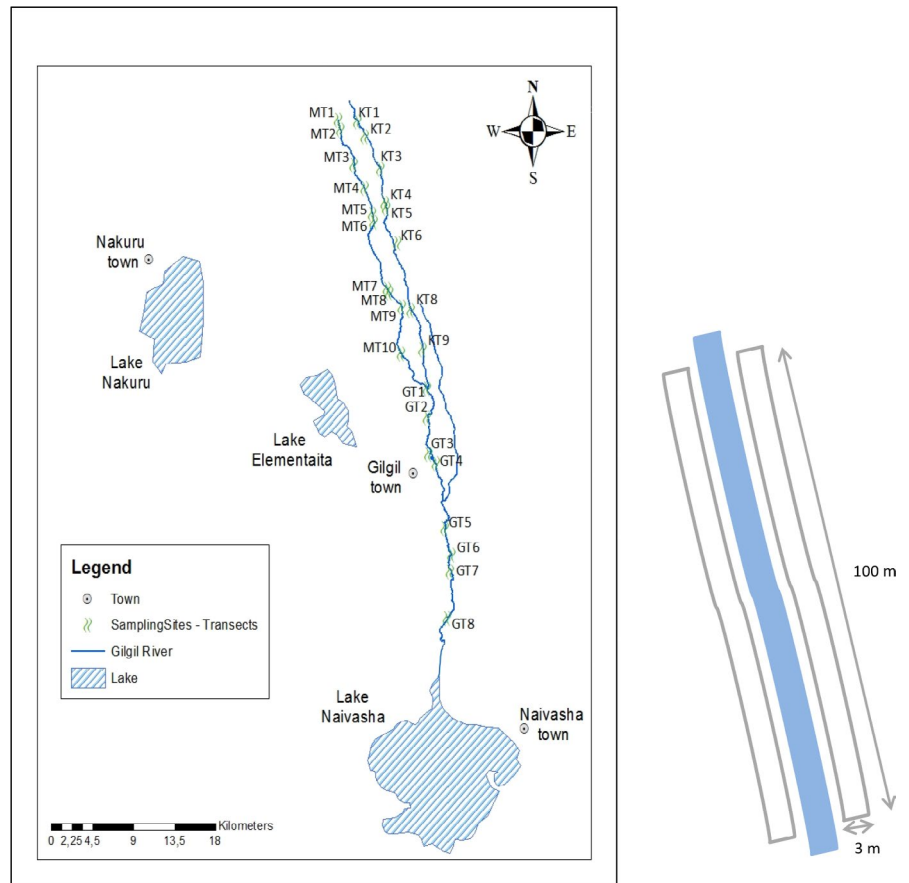
Transect surveys were carried out in February 2018 and in September 2019 by recording tree species above 1 m height in 26 sites. At each site, two belt transects were laid, one on each side of the river channel. Each transect was 100 m long and 3 m wide, parallel to the river and adjacent to the edge of the active river channel (Figure 2). The total surface area assessed was 3300 m² (quadrats) and 15,600 m² (transects) for the 88-km-long riparian corridor (Morendat 30 km, Kiriundu 32 km, Gilgil 26 km). The total number of quadrats and transects was dictated by available time and resources. Regarding quadrats, limited accessibility to the upper catchment sites implied that the Gilgil section ended having a larger number of sampling sites per linear river length.

Species identification was based on Agnew (2013), Beentje (1994), Beentje et al. (1954–2012) and Maundu et al. (2005). Nomenclature and authorities were derived from Plants of the World Online (POWO).

2.4 | Species categorisation

Species were assigned to the following categories: (1) habitus (herb, shrub, tree); (2) origin (native, introduced); (3) chorotype (Rift Valley, Tropical East Africa, Tropical Africa, Pantropical, Cosmopolitan); and (4) habitat occurrence (Cultivation, Bushland, Woodland, Forest, Forest edge, Riverine) following Beentje et al. (1954–2012).

FIGURE 2 Location of tree transect sites along the Gilgil River and tributaries (Morendat and Kiriundu). On the right: a diagram representing the positioning of transects at each site, for the assessment of trees and shrubs



2.5 | Community analysis

Vegetation quadrat and tree transect taxa presence data, considered separately, were analysed in R v. 4.0.2 (R Core Team, 2020). Sample groups were defined by hierarchical agglomerative clustering (complete linkage) based on Jaccard distance, tested by analysis of similarity and further assessed by Non-metric Multi-Dimensional Scaling ordination (Bray–Curtis rank similarities) tested with Permanova (999 permutations) after checking for homogeneity of multivariate dispersion. Altitude contour lines were plotted within the NMDS ordination axes space using R ‘vegan package’ (Oksanen et al., 2016).

Lithology, soils and land use can be key determinants of species composition in riparian corridors (Nucci et al., 2012). The Nakuru County atlas of agro-ecological zones (Jaetzold et al., 2006) allowed us to assign a physiographic/lithological category to each site according to its location. In the upstream, two categories were included as follows: (1) UPB1 well-drained deep luvisols developed over volcanic ashes, overlying basalt and nepheline tuffs, with inclusions of gleyic soils; (2) RB3 deep friable eutric nitisols developed from basalt, nepheline and phonolite tuffs. Two categories were included in the downstream: (3) P1PC—imperfectly drained sandy cambisols mostly developed from ancient lake sediments laying over pyroclastic rocks, (4) PIU1—very deep poorly drained moderately sodic solonetz developed over lacustrine plains. These

categories were fitted as vectors in NMDS ordinations; vector significance was assessed by *envfit* (R ‘vegan’ package Oksanen et al., 2016; Strohbach et al., 2009).

Indicator species analysis was carried out with R *indicspecies* (De Cáceres et al., 2020) using the function *Indval*, which ranks species according to *specificity* (predictive value of the species as indicator of the site group) and *sensitivity* (probability of finding the species in sites belonging to the same group). We used the R *multipatt* function to calculate Pearson's ϕ coefficient of association, which is a correlation index used to order species among alternative site groups according to *fidelity*, defined as a measure of species concentration in vegetation units (Chytrý et al., 2002). This gave additional confirmation. *Indval* reflects species partitioning by groupings set by the observer, and ϕ is obtained by comparing the taxa to the rest of the dataset. This index is less prone to bias than *Indval* when species occurrence is low in relation to total species number (Chytrý et al., 2002) as in our data. As an additional feature, Pearson's ϕ coefficient of association can express taxa avoidance of a given site, and it can identify taxa that tend to be euryoecious; that is, rather than being associated with a particular group, they tend to have the highest score in the set of all sites.

Longitudinal distribution of origin, chorology, habitat occurrence and total richness per group were assessed by Spearman rank correlation between altitude and the percentage of species belonging to each category. Critical p values were Holm–Bonferroni adjusted (type I error increase due to multiple testing).

2.6 | Diversity

The contribution to regional biodiversity (γ diversity) can be considered as the sum of the taxa present at each site (α diversity) added to the extent of change in composition between sites (β diversity; Gering et al., 2003). Assessing separate components of β diversity (species turnover and species replacement between single sites) can lead to insights about processes that influence succession along gradients. The methodology adopted to obtain β diversity was based on estimates of 'spatial turnover' (β_{sim}) and 'nestedness' (β_{nes}) components derived from Simpson's and Sørensen's (β_{sor}) dissimilarity indices ($\beta_{sor} = \beta_{sim} + \beta_{nes}$; Baselga, 2010), calculated with *betapart* R package (Baselga, 2018). This method focusses on changes in diversity components between adjacent sites.

Averages of pairwise comparisons among single sites were used to obtain estimates of change in diversity between site groups (e.g. 'upstream quadrats' compared with 'downstream quadrats'). This method disregards taxa that are shared among pairs (Baselga, 2010; Legendre, 2014). So, to obtain change in diversity between groups we adopted the method recently introduced by Fortin et al. (2020a, 2020b; *betadiv*). Fortin et al. defined statistical estimators of β diversity indices based on Baselga's (2010) work, adapted them to multiple-site calculations and adjusted them to avoid potential bias produced by comparing populations of different sizes (Fortin et al., 2020a, 2020b). The algorithm calculates also estimates of α and γ diversities. To account for heteroscedasticity and unequal sample size, the calculated multiple-site β diversity components ($\beta_{sor} = \beta_{sim} + \beta_{nes}$; as suggested by Fortin et al. (2020a) multiple-site β diversity components are indicated with uppercase subscripts) were compared between each other using Welch's *t* test (Welch, 1947).

3 | RESULTS

3.1 | Land-use classification and riparian condition

The Gilgil sub-catchment is highly modified. It is covered mainly by extensively cultivated farmland (44%) and Dry wooded grassland (28%) used as extensive pasture (Figure 3). The rest of the sub-catchment includes Bushland (14%), Forest (4%), Intensively cultivated farmland (4%), Wetlands (3%), and Settlements (3%). The largest remaining portion of undisturbed Afromontane forest consists of a 0.32 km² *Juniperus procera* Hochst. ex Endl. forest that we visited in the proximity of site M6 along the Morendat. The lower section of the catchment is characterised by a mosaic of Bushland and Wooded grassland. Along the whole river basin, human settlements are positioned high above steep riverbanks, with few farms directly beside the channel.

3.2 | Taxonomic characterisation

Quadrats recorded 348 taxa (Appendix S1), 312 (93%) were identified to species level and 21 to genus; 15 taxa remained unidentified and are

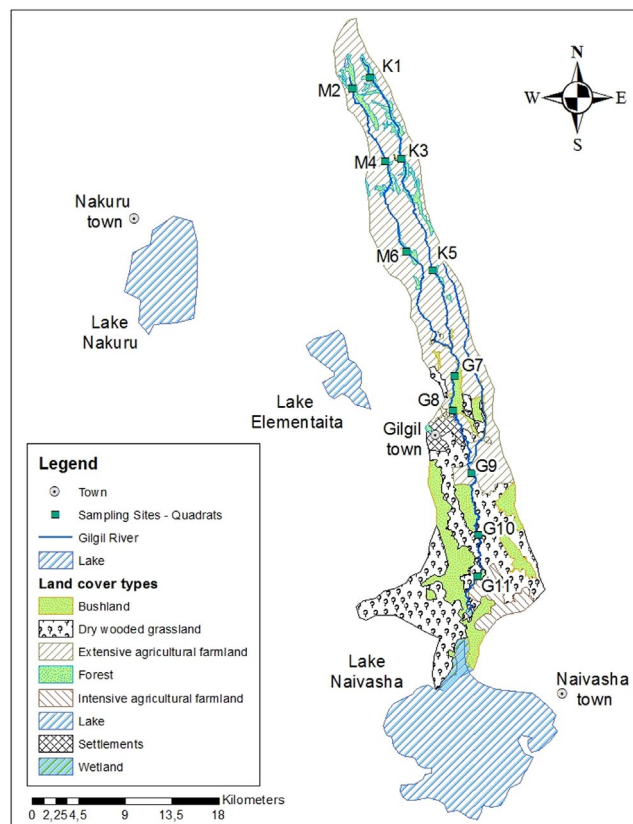


FIGURE 3 Gilgil basin land-use map obtained by interpretation of Google Earth satellite images captured in April 2017

not reported. We recorded 75 families—Asteraceae (46 sp.), Poaceae (25 sp.), Fabaceae (20 sp.), Acanthaceae (20 sp.), Lamiaceae (14 sp.), Malvaceae (16 sp.) and Rubiaceae (11 sp.) had >10 taxa. The mean number of taxa per quadrat was 55. On average, 16 species (4.7%) were endemic to the eastern Rift Valley highlands and 33 (9.8%) introduced.

Transects recorded 83 taxa (Appendix S2), with seven unidentified and not reported. Twenty-one of these were not found in the quadrats (indicated by * in Appendix S2). The 76 identified species belonged to 35 families and 59 genera. The richest family was Fabaceae (8 spp.), followed by Anacardiaceae, Araliaceae, Euphorbiaceae, Malvaceae and Salicaceae, which contained four species each. Seven species were endemic to the East African Highlands and to the Rift Valley, while seven were introduced. Transect KT7, placed in the lower portion of the Kiriundu, consisted of a monospecific plantation of *A. mearnsii* and was excluded from any further analysis.

Overall, between 1/4 and 1/2 of the taxa in a single site, regardless if assessed by quadrats or transects, belonged to species that are known from the taxonomic literature to be broadly distributed throughout tropical Africa. 'Riverine' taxa (i.e. adapted to growth in stream corridors) represented 15% of the total number of taxa present in both quadrats and transects. Introduced taxa amounted to 13% in quadrats and 11% in transects, while Rift Valley endemics averaged 3% in quadrats and 10% in transects. Finally, most of the remaining taxa were pantropical and cosmopolitan. Species occurring in >75% of the quadrats included the following: *Achyranthes aspera* L. a common

East African species; *Hypoestes forskoolii* (Vahl.) R. Br. widely distributed, toxic, common throughout tropical Africa and the Arabic peninsula, *Zehneria scabra* (L.f.) Sond. a riverine vine common throughout the tropical and subtropical Old World and *Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes., a spiny riverine shrub common throughout Africa and the Arabic peninsula. The commonest tree was *Olea europaea* subsp. *africana* (Mill.) P.S.Green, which was recorded in 3/4 of the tree transects. Overall, approximately 1/3 of all taxa were recorded only once.

3.3 | Group subdivision

The cluster dendrogram (Figure 4) identified two main groups from the eleven sites produced by quadrat sampling: (1) upstream (quadrats K1, M2, K3, M4, K5, M6, from 2700 to 2300 m); (2) downstream (quadrats G7, G8, G9, G10, G11, from 2100 to 1900 m). Almost half (153; 44.5%) of the species were recorded exclusively in the six sites located in the upper catchment, while 116 (34.7%) were restricted to the five lower catchment sites; the overall number of species per group was similar, and fewer species (65, 19.5%) were shared between the two groups (the frequencies of species shared by the two groups differed significantly from those exclusive of the upper catchment and of the lower catchment; $\chi^2 = 35.2$, $df = 2$, $p < .001$). The dendrogram and the NMDS plot (999 permutations, $p < .001$; Figure 5) showed an internally heterogeneous composition. R *ordisurf* fitting of altitudinal data within the ordination plot suggested a consistent relationship between altitude and the main ordination axis.

A second cluster analysis subdivided tree transects into three groups (Figure 6): upstream (MT1, MT2, MT3, MT4, MT8, KT1, KT2, KT4, KT5, from 2700 to 2500 m); midstream (MT5, MT6, MT7, MT9, MT10, KT3, KT6, KT8, KT9 from 2600 to 2200 m) and downstream (GT1 to GT8, from 2200 to 1900 m). The NMDS plot (Figure 7) showed a slight overlap between the first two groups, although Permanova confirmed that the subdivision was highly significant (999 permutations, $p < .001$). Twelve species (15.8%) were shared among groups.

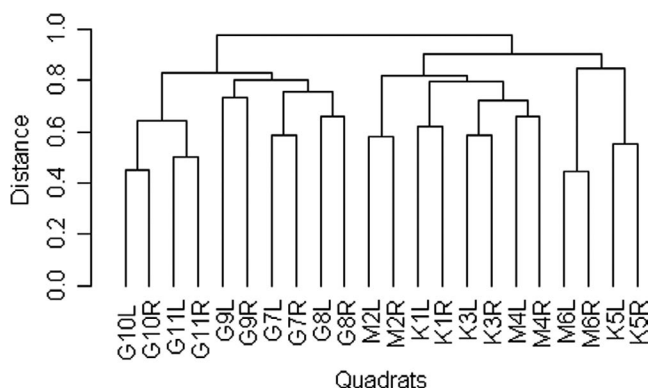


FIGURE 4 Hierarchical cluster dendrogram, Jaccard distance (complete linkage), based on vegetation quadrats data. ANOSIM ($p < .001$; $R = 0.978$). G, Gilgil river; M, Morendat river; K, Kiriundu river; R, Quadrat on right river bank; L, quadrat on left river bank. Two clusters were selected (cut-off at 0.92)

3.4 | Indicator species

Indicator species analysis identified 70 taxa significantly associated with either quadrat group (34 upstream and 36 downstream) according to *specificity* and *sensitivity* scores; a selection of the taxa most significantly associated with the groups is illustrated in Table 1. Upstream sites were characterised by typical forest taxa, such as *Rhamnus prinoides* L'Hér., *Asplenium stuhlmannii* Hieron. and *Sanicula elata* Buch.-Ham. ex D.Don, and by species typical of forested riverine corridors, such as *Jasminum abyssinicum* Hochst. ex DC. and *Myrsine melanophloeos* (L.) R.Br. ex Sweet. Downstream sites were dominated by woodland species adapted to mesic/xeric conditions such as *Grewia similis* K. Schum., *Pavonia burchellii* (D.C.) R.A.Dyer, *Maerua triphylla* A. Rich. and *Mystroxydon aethiopicum* (Thunb.) Loes. Taxa adapted to overgrazed areas and to disturbed riparian zones were also distinctive of the downstream quadrat group. These included *Sida tenuicarpa* Vollesen, *Acalypha volkensii* Pax, *Setaria verticillata* (L.) P. Beauv. and *Ocimum gratissimum* L. Strictly riverine species achieved low ranks as indicator taxa; they included *Senna didymobotrya* (Fresen.) H.S.Irwin & Barneby, *Celtis africana* Burm.f., *Cyperus dichrostachyus* Hochst. ex A.Rich. and *Cyperus exaltatus* Retz. Further attributes of *multipatt* identified 33 taxa that tend to be euryoecious, as they were least associated with a particular group (Appendix S3).

Indval identified 21 taxa associated with one of the groups and nine associated with group combinations (1 upstream, 4 midstream and 16 downstream), out of 76 taxa recorded by tree transects. The ranking of indicator taxa obtained with both methods (*Indval* and Pearson's ϕ coefficient of association) gave a close match (Table 2). *E. globulus* scored highest in the upstream group, highlighting the importance of tree plantations in the upstream riparian corridor. Similarly, *A. mearnsii* appeared as an indicator in midstream and *H. lusitanica* as first rank of the combination between upstream and midstream. Highly indicative of the downstream was the riparian *Dombeya burgessiae* Gerrard ex Harv. & Sond., but next to it were several taxa adapted to xeric biotopes, such as *M. triphylla*, *Tarchonanthus camphoratus* L., *Euclea divinorum* Hiern., *Euphorbia candelabrum* Welw., *G. similis* and *Vachellia abyssinica* (Hochst. ex Benth.) Kyal. & Boatwr. Riparian species such as *Salix mucronata* Thunb., *Sesbania sesban* (L.) Merr. and *Ficus sur* Forssk. achieved lower rank. Among the taxa least associated with particular groups (Appendix S4), the riparian *G. heterophylla* and forest species, such as *J. procera*, *O. europaea* subsp. *africana* and *Pittosporum viridiflorum* Sims, were part of the corridor all along from headwaters to downstream.

3.5 | Longitudinal correlation

There were significant relationships between altitude and species distribution, taking into consideration categories related to chorotype (five categories), habitat occurrence (six categories) and origin (native/introduced) (Table 3), but sometimes with contrasting results between transects and quadrats. 'Forest' correlated positively with altitude, but 'Woodland' and 'Bushland' showed a negative correlation with altitude in both quadrats and transects. Quadrats indicated

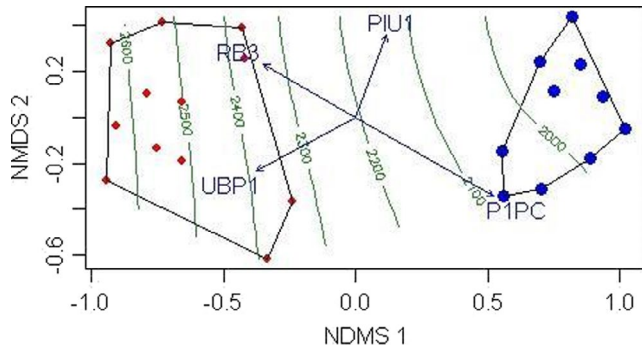


FIGURE 5 Non-metric Multi-Dimensional Scaling of quadrat data (stress: 0.095); sites are clearly divided into two groups (upstream on the left, downstream on the right, Permanova 999 permutations $p < .001$). Physiographic/lithological UBPI and P1PC (see main text) vectors correlated significantly with NMDS axes. Altitude contours (m a.s.l.) were fitted using R *ordisurf*

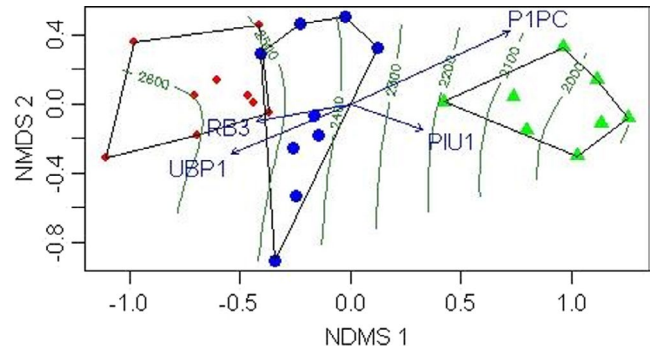


FIGURE 7 Non-metric Multi-Dimensional Scaling of transect data (stress: 0.133); sites are clearly divided into three groups (upstream on the left, midstream and downstream on the right, Permanova 999 permutations $p < .001$). Physiographic/lithological UBPI and P1PC (see main text) vectors correlated significantly with NMDS axes. Altitude contours (m a.s.l.) were fitted using R *ordisurf*

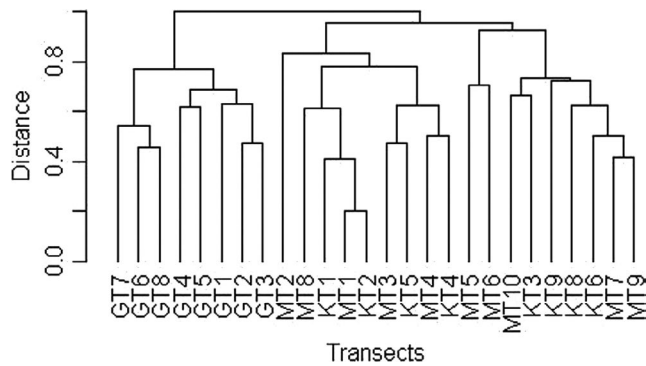


FIGURE 6 Hierarchical cluster dendrogram, Jaccard distance (complete linkage), based on tree transects data; ANOSIM $p < .001$; $R = 0.781$. G, Gilgil; M, Morendat, K, Kiriundu, T, Transect. Three clusters were selected (cut-off at 0.95)

a downstream increase in taxa belonging to the chorotypes ‘Tropical East Africa’ and an upstream increase in ‘Rift Valley’ and ‘Native’ taxa (just below α adjusted significance). Transects (but not quadrats) revealed a significantly negative correlation between altitude and ‘Riverine’ taxa. The total number of species showed a significant negative correlation with altitude in transects, but no pattern was detected with quadrats. The number of introduced taxa showed no change between upstream and downstream.

3.6 | Community composition

3.6.1 | The upstream riparian community

The upstream section was ‘Afro-montane single-dominant *J. procera* forest (Fbj)’, but a large proportion has been modified to accommodate cultivation. The upstream riparian corridor hosted vegetation characterised mainly by forest and riverine forest taxa, as highlighted by the indicator species recorded in vegetation quadrats (Table 1). This

distribution pattern was strengthened by a highly significant positive correlation between forest taxa and altitude detected in quadrats and in transects (Table 3). Taxa endemic to the Rift Valley present in the upstream in both quadrats and transects mostly included forest species and riverine trees such as *Dombeya torrida* (J.F.Gmel.) P.Bamps, *Vitex fischeri* var. *keniensis* (Turill) Meerts, *Vachellia gerrardii* Benth. P.J.H. Hurter, *Ethulia vernonioides* (Schweinf.) M.G. Gilbert, *Geranium kilimandscharicum* Engl, *Impatiens meruensis* Gilg, *Crotalaria agatiflora* Schweinf. and *Dryopteris tricellularis* J.P.Proux. Quadrat samples indicated that the percentage of taxa originating within the Rift Valley was significantly correlated with higher altitude (Table 3); Tropical East African taxa showed a reverse pattern.

Exotic taxa were present in all quadrats and in all transects. Several exotic herbs, shrubs and aquatic macrophytes were recorded in upstream quadrats. These were *Calceolaria mexicana* Benth., *Cestrum aurantiacum* Lindl., *Erica arborea* L., *Galium spurium* L., *Passiflora mollissima* (Kunth) L.H.Bailey, *Phalaris arundinacea* L., *Persicaria nepalensis* (Meisn.) H.Gross and *Polystichum sinense* (Christ) Christ. None of these were highlighted as indicator species. Upstream and midstream transects were instead characterised by the frequent presence of plantations of a small number of exotic tree species, sometimes up to the riverbank, as highlighted by indicator species analysis.

3.6.2 | The downstream riparian community

In the lower catchment, characterised by a warmer and drier climate, corresponding to ‘Evergreen and semi-evergreen bushland and thicket (Be)’, we recorded woodland and bushland species adapted to mesic/xeric conditions, as well as taxa adapted to overgrazed areas and to disturbed riparian zones. There was also a significant negative correlation between altitude and the proportion of woodland and bushland taxa, both in quadrats and in transects. Quadrat data also indicated that the proportion of native taxa was positively correlated to altitude (Table 3). Despite this, in places characterised

TABLE 1 Ranking of indicator species identified through *multipatt* (R 'indicspecies') using vegetation quadrat data according to φ and *Indval* statistics. Specificity and sensitivity are components of *Indval* and are given scores between 0 and 1. Only the most significant ($p < .01$) has been retained (cut-off set at 0.6 φ value)

	φ	<i>Indval</i>	Specificity	Sensitivity
Upstream				
<i>Jasminum abyssinicum</i> Hochst. ex DC.	1	1	1.0	1.0
<i>Rhamnus prinoides</i> L'Hér.	2	2	1.0	0.9
<i>Asplenium stuhlmannii</i> Hieron.	3	3	1.0	0.8
<i>Myrsine melanophloeos</i> (L.) R.Br. ex Sweet	4	4	1.0	0.8
<i>Adiantum poiretii</i> Wikstr.	5	5	1.0	0.7
<i>Sanicula elata</i> Buch.-Ham. ex D.Don	6	6	1.0	0.7
<i>Dombeya torrida</i> (J.F.Gmel.) P.Bamps	7	7	0.9	0.8
<i>Crassocephalum montuosum</i> (S.Moore) Milne-Redh.	8	9	1.0	0.7
<i>Sonchus schweinfurthii</i> Oliv. & Hiern	9	10	1.0	0.7
<i>Asplenium monanthes</i> L.	10	11	1.0	0.6
<i>Clusia kilimandscharica</i> Engl.	11	12	1.0	0.6
<i>Hypericum revolutum</i> Vahl	12	13	1.0	0.6
<i>Nuxia congesta</i> R.Br. ex Fresen.	13	14	1.0	0.6
<i>Prunus africana</i> (Hook.f) Kalkman.	14	15	1.0	0.6
<i>Olea europaea</i> subsp. <i>africana</i> (Mill.) P.S.Green	15	8	0.8	0.8
Downstream				
<i>Grewia similis</i> K. Schum.	1	1	1.0	1.0
<i>Pavonia burchellii</i> (D.C.) R.A.Dyer	2	2	0.9	1.0
<i>Maerua triphylla</i> A. Rich.	3	3	1.0	0.8
<i>Sida tenuicarpa</i> Vollesen	4	4	1.0	0.8
<i>Acalypha volkensii</i> Pax	5	7	1.0	0.7
<i>Mystroxydon aeathropicum</i> (Thunb.) Loes.	6	8	1.0	0.7
<i>Hemionitis viridis</i> (Forssk.) Christenh.	7	9	1.0	0.7
<i>Pterolobium stellatum</i> (Forssk.) Brenan	8	10	1.0	0.7
<i>Ocimum gratissimum</i> L.	9	5	0.9	0.8
<i>Alternanthera pungens</i> Kunth	10	13	1.0	0.6
<i>Commelina diffusa</i> Burm.f.	11	14	1.0	0.6
<i>Fuerstia africana</i> T.C.E. Fr.	12	15	1.0	0.6
<i>Lepidium bonariense</i> L.	13	16	1.0	0.6
<i>Psiadia punctulata</i> Vatke	14	17	1.0	0.6
<i>Senecio hadiensis</i> Forssk.	15	18	1.0	0.6
<i>Setaria verticillata</i> (L.) P. Beauv.	16	19	1.0	0.6
<i>Ehrharta erecta</i> Lam.	17	6	0.7	1
<i>Gutenbergia boranensis</i> (S.Moore) M.G.Gilbert	18	11	0.9	0.7

by greater continuity of the riparian vegetation belt, several forest taxa, such as *J. procera* and *O. europaea* subsp. *africana*, as well as few herbs and climbers typical of humid forests, stood in striking contrast to the dry *Acacia* bush that covered most of the lower valley, just beside the stream corridor. In the downstream riparian community, forest taxa represented on average 12% of the taxa encountered in quadrats and 29% of the taxa encountered in transects.

In this downstream community, quadrats and transects provided a contrasting perspective concerning strictly riverine taxa. In downstream quadrats, riverine taxa represented on average only 14%

(8%–18%) of the taxa encountered and included *Hypericum roeperianum* G.W. Schimp. ex A.Rich. and *Syzygium cordatum* Hochst. ex Krauss. In contrast, riverine species were 26% (16%–37%) of the taxa encountered in downstream transects and included riverine trees that were uncommon upstream. This result was supported by the indicator analysis and further highlighted by a significant negative correlation between riverine taxa and altitude in transects but not in quadrats (Table 3).

The downstream group included fewer endemics in relation to upstream. They were as follows: *Aloe kedongensis* Reynolds, *E. vernonioides* and *D. burgessiae*. Downstream, exotic species differed

TABLE 2 Ranking of indicator species identified through multipatt (R 'indicspecies') using the tree transect data according to φ and *Indval* statistics. Specificity and sensitivity are components of *Indval* and are given scores between 0 and 1. Only the most significant ($p < .01$) has been retained (cut-off set at 0.6 φ value)

	φ	<i>Indval</i>	Specificity	Sensitivity
Upstream				
<i>Eucalyptus globulus</i> Labill.	1	1	1.0	0.6
Midstream				
<i>Maesa lanceolata</i> Forssk.	1	2	1.0	0.7
<i>Acacia mearnsii</i> De Wild.	2	1	0.9	0.8
<i>Rhamnus staddo</i> A.Rich.	3	4	1.0	0.4
Downstream				
<i>Dombeya burgessiae</i> Gerrard ex Harv. & Sond.	1	1	1.0	1.0
<i>Maerua triphylla</i> A. Rich.	2	2	1.0	0.9
<i>Tarchonanthus camphoratus</i> L.	3	3	0.8	1.0
<i>Euclea divinorum</i> Hiern.	4	4	1.0	0.7
<i>Euphorbia candelabrum</i> Welw.	5	5	1.0	0.7
<i>Salix mucronata</i> Thunb.	6	6	1.0	0.7
<i>Vachellia abyssinica</i> (Hochst. ex Benth.) Kyal. & Boatwr.	7	7	1.0	0.7
<i>Grewia similis</i> K. Schum.	8	8	1.0	0.6
<i>Pterolobium stellatum</i> (Forssk.) Brenan	9	9	1.0	0.6
<i>Sesbania sesban</i> (L.) Merr.	10	10	1.0	0.6
<i>Ficus sur</i> Forssk.	11	12	1.0	0.5
<i>Toddalia simplicifolia</i> Engl.	12	13	1.0	0.5
<i>Vachellia xanthophloea</i> (Benth.) Galasso & Banfi	13	14	1.0	0.5
<i>Cussonia holstii</i> Harms ex Engl.	14	11	0.8	0.6
Upstream/Midstream				
<i>Hesperocyparis lusitanica</i> (Mill.) Bartel	1	3	1.0	0.7
<i>Dombeya torrida</i> (J.F.Gmel.) P.Bamps	2	1	0.9	0.8
<i>Hypericum revolutum</i> Vahl	3	2	0.9	0.8
<i>Nuxia congesta</i> R.Br. ex Fresen.	4	4	1.0	0.7

from those present in the catchment upstream and included the following: (1) several widely distributed weeds found in downstream quadrats that dispersed from upstream cultivated plots, such as *Chenopodium opulifolium* Schrad. ex W.D.J. Koch & Ziz, *Chlorophytum viridescens* Engl., *Erigeron bonariensis* L., *Cotula australis* Hook.f., *Galinsoga parviflora* Cav., *S. verticillata*, *Sonchus oleraceus* L. and *Tagetes minuta* L. and (2) a small number of exotic trees and shrubs found in both quadrats and transects: *A. mearnsii*, *Grevillea robusta* A.Cunn. ex R.Br., *Dovyalis caffra* (Hook.f. & Harv.) Warb. and the succulent *Opuntia ficus-indica* (L.) Mill.

3.7 | Environmental filtering

Lithology vectors were significantly correlated to the NMDS axes that determined the ordination of samples into groups (Table S1). Upstream, samples were significantly associated ($R^2 = 0.34$, $p = .020$ and $R^2 = 0.33$, $p = .012$; quadrats and transects, respectively) to UBP1 physiographic/lithological category. In the lower portion of

the catchment, the species assemblage significantly correlated with the presence of soils of the P1PC category ($R^2 = 0.69$, $p < .001$ and $R^2 = 0.613$, $p < .001$; quadrats and transects, respectively). The remaining categories at the margins, upstream RB3 and downstream PIU1, had a significant but weaker (in relation to P1PC) statistical correlation with the distribution of our quadrats; this reflected in lower coefficients of determination (for RB3, $R^2 = 0.306$, $p = .032$; for PIU1, $R^2 = 0.251$, $p = .039$). In the case of transects, the relationship was not statistically significant ($R^2 = 0.306$, $p = .032$ and $R^2 = 0.251$, $p = .039$).

3.8 | β diversity

High pairwise dissimilarity was detected between geographically distant samples, and the least difference was between left and right quadrats belonging to the same site (data not shown). In general, spatial replacement (β_{sim}) dominated the overall score (β_{sor}). Between pairs of quadrats, the β_{nes} component contributed up to 19%. With

transects, high nestedness ($\beta_{nes} = \beta_{sor} = 0.5$) was detected between the two highest samples along the Morendat. In the rest of the longitudinal profile, pairwise β diversity followed a highly irregular pattern.

Multiple-site β diversity computed for quadrats and transects (Tables 4 and 5, first row) included estimates of the entire riparian corridor surface, that is the surface of quadrats/transects that would be required to sample the entire riparian corridor using the sampling design defined in this study. Observed species density was almost identical for the two quadrat groups (upstream and downstream). With transects, the total number of species and species density increased from the sources to the mouth. The estimate of γ diversity calculated by the algorithm (Tables 4 and 5) is significantly higher than the number of taxa reported. Analysis of multiple-site β diversity between groups shows, in all cases, a highly significant difference between groups in the Sørensen and

nestedness components, but no difference in Simpson index (spatial turnover), which dominated the overall species replacement. The significance of all tests was well beyond type I error inflation due to multiple comparisons. Overall, multiple-site β diversity (β_{sor}) was 0.419 ± 0.003 for quadrats and 0.409 ± 0.010 for transects, of which 15% and 20%, respectively, was represented by nestedness (β_{nes}) and the rest by spatial replacement.

4 | DISCUSSION

4.1 | Broad patterns of species distribution

The species composition of the Gilgil plant community resembles the one reported by White (1983) and communities reported along River Njoro by Mathooko and Kariuki (2000), who distinguished a 'Montane' vegetation (above 2200 m a.s.l.), from a 'Submontane' (below 2200 m a.s.l.). Our study offered greater species composition detail, with quadrats and transects providing a different and complementary representation. Sampled quadrats covered a small surface area but with detailed mapping of the entire local plant community. The recording of taxa along transects focussed on trees and shrubs and covered a relatively high proportion of the stream corridor in shorter time. Transects allowed us to increase the surface surveyed and to better characterise the distribution of trees at a broader scale (Sarr & Hibbs, 2007). Adding the transects to the quadrats survey increased the overall number of taxa encountered.

Over 100 taxa, nearly one third of all taxa encountered during our study (quadrats and transects combined), were recorded only once. This is likely to be an underestimate of the true diversity. This conclusion is coherent with the small surface area sampled (0.019 km^2) in relation to the surface area of the entire riparian corridor (*ca.* 3.4 km^2) and with the proportion between the (low) number of samples and the (high) number of taxa, which indicated high α diversity. This could suggest that several species tend to have a restricted distribution, which could be a reflection of the ongoing degradation and fragmentation of the corridor vegetation.

TABLE 3 Relationship between altitude and species descriptors: taxa origin, chorotype and habitat, as indicated by Spearman rank correlation. Significance was Holm–Bonferroni adjusted for multiple testing (α -quadrats: 0.00417, α -transects: 0.005)

	Altitude	p Value
Quadrats		
Tropical Africa	0.732	.00011
Tropical East Africa	−0.718	.00017
Rift Valley	0.680	.00049
Forest	0.856	$3.6 \cdot 10^{-7}$
Woodland	−0.923	$9.6 \cdot 10^{-10}$
Bushland	−0.636	.00147
Native	0.696	.00032
Transects		
Forest	0.730	.00002
Riverine	−0.716	.00003
Woodland	−0.735	.00001
Bushland	−0.685	.00008
Number of taxa	−0.616	.00062

TABLE 4 Estimated multiple-site Simpson, Sørensen and Nestedness in upstream Afromontane riparian and in downstream highland riparian vegetation quadrats (\pm SE); p values refer to the significance of Welch's test

	Upstream	Downstream	p Value
Entire riparian corridor surface area (m^2)	2,640,000	780,000	
Surface area sampled (m^2)	12,400	5200	
Number of quadrats	12	10	
Number of taxa observed	218	180	
Species density (spp. m^{-2})	0.121	0.120	
Estimated α	57.9 (± 4.853)	52.4 (± 4.662)	<.001
Estimated γ	301.7	256.2	
Simpson	0.303 (± 0.151)	0.285 (± 0.144)	.385
Sørensen	0.378 (± 0.010)	0.361 (± 0.009)	<.001
Nestedness	0.075 (± 0.012)	0.076 (± 0.015)	<.001

TABLE 5 Estimated multiple-site Simpson, Sørensen and Nestedness in upstream, midstream and downstream tree transects (\pm SE); p values refer to the significance of Welch's test

	Upstream	Midstream	Downstream	Up-Mid p value	Mid-Down p value
Entire corridor surface (m ²)	134,907	219,090	168,000		
Surface sampled (m ²)	5400	5400	4800		
Number of transects	18	18	16		
N taxa observed	28	44	54		
Species density (spp. m ⁻²)	0.010	0.016	0.023		
Estimated α	11.9 (\pm 1.195)	16.7 (\pm 1.280)	21.2 (\pm 1.839)	<.001	<.001
Estimated γ	33.359 (\pm 5.336)	53.296 (\pm 6.798)	95.201 (\pm 25.745)	<.001	<.001
Simpson	0.204 (\pm 0.036)	0.280 (\pm 0.028)	0.241 (\pm 0.038)	.118	.429
Sørensen	0.302 (\pm 0.028)	0.343 (\pm 0.026)	0.314 (\pm 0.015)	<.001	<.001
Nestedness	0.098 (\pm 0.033)	0.063 (\pm 0.022)	0.073 (\pm 0.024)	<.001	<.001

4.2 | Diversity at multiple scales

At a larger landscape scale, riparian corridors are important contributors to regional biodiversity, particularly in drier regions where they constitute a strong discontinuity with the surrounding landscape (Sabo et al., 2005). At the scale of the riparian corridor as a whole, plant diversity tends to be shaped by the interplay of landscape and local scale fluvial patterns and processes. The former include soil type, rainfall, temperature and potential evaporation. At local scale, longitudinal differences in species composition and the maintenance of a diversity gradient with the (up-slope) community external to the corridor tend to be determined by fluvial processes, such as flooding and scouring (Sarr & Hibbs, 2007), that are more effective in large rivers, for example the Tana River described by Hughes (1988), than in smaller streams (Tabacchi et al., 1996). To investigate the dominant diversity patterns, our analysis focused on longitudinal species change through a comparison between groups of quadrat and transect records assessed by ordination techniques and by separation of the β diversity components reflecting assemblage nestedness and spatial species turnover.

4.2.1 | The landscape scale

Before the advent of agriculture, the upper river terraces used to be covered by forests belonging to the potential 'Afromontane forest (Fbj)' group. The corridor hosts remnants of these pristine forest taxa that find shelter between the riverbank and the river terrace because of steep slopes, rocky outcrops, sudden changes in altitudinal level (steps and cascades) and/or waterlogging that prevent easy agricultural exploitation. In the upstream, in the absence of human impact, the species gradient between the riparian corridor and the lateral uplands would have been low, but has increased because of agricultural exploitation.

Downstream sites host few riverine herbs, climbers and several trees absent in the surrounding dry *Acacia-Commiphora* woodland and *Tarchonanthus* dominated savanna covering the Rift Valley floor,

which represent a fire/overgrazing degradation stage of the potential 'Evergreen and semi-evergreen bushland and thicket (Be)'. In this lower floodplain, the riparian corridor still maintains a naturally strong microclimatic gradient with the surrounding landscape that generates a high species turnover between the corridor and the valley slopes. This effect is known to increase under dry climate (Sabo et al., 2005), such as the Rift Valley floor, which faces strong evaporation deficit (Odongo et al., 2015). This lateral diversity gradient appeared to be reinforced by a partial colonisation of downstream sites by 'upstream taxa'. Several Afromontane taxa, such as *J. procer*, that typically grow at an average rainfall of 700–1500 mm year⁻¹ (Bussmann, 2001) extended their distribution towards lower elevation. This indicated that the riparian corridor provides ideal conditions such as substrate and microclimate that tend to expand the distribution of Afromontane forest species towards the lowlands.

4.2.2 | Internal species turnover

Stream corridor fragmentation can be a major cause of biodiversity loss (Tilman et al., 2001) by widening gaps, modifying the microclimate and facilitating the establishment and the dispersion of exotics (Pyšek & Richardson, 2007; Turner, 1996). In the upper catchment, fragmentation was mainly caused by conversion to plantation and crops, while downstream it was caused by grazing and trampling, causing compaction and erosion (also described by Agouridis et al., 2005; Dunne et al., 2011; Sarr, 2002). Grazing severely affects plant regeneration in the Afromontane environment (Kikoti et al., 2015; Wassie et al., 2009).

Agricultural encroachment, cattle ranching and charcoal burning have a noticeable impact on the Gilgil stream corridor vegetation, but they did not overwhelm the natural pattern of species succession. As highlighted by pairwise (sample by sample) and multi-site (group by group) β diversity analysis, and despite separation into groups, longitudinal changes in species assemblage reflected a steady progressive spatial turnover along the altitudinal gradient rather than a

pattern that could be attributed to loss of species belonging to an original nested assemblage. This evidence suggests that landscape scale drivers that create a strong polarisation between the upstream and the downstream vegetation within the catchment are moderated by local scale processes that tend to determine a gradual longitudinal diversity change. The effect of these processes persists despite pervasive anthropogenic impact.

4.3 | The downstream floodplain

The difference in taxonomic richness noticed in transects between upstream and downstream is related to a biodiversity decrease in the upper catchment caused by anthropogenic activities, such as charcoal burning and exotic tree plantations. In the lower basin, the increase in richness was accompanied by the appearance of a specialised floodplain community represented by trees such as *F. sur*, *S. sesban*, *Vachellia xanthophloea* (Benth.) Galasso & Banfi associated with 'Riverine wooded vegetation (R)' (van Breugel et al., 2015) and *S. mucronata*. In this lower section of the Gilgil, signs of channel incision and floodplain narrowing are common, despite non-significant changes in the amount of precipitation during the last five decades (Odongo et al., 2015). As elsewhere in East Africa, these impacts are likely caused by upstream deforestation, which leads to overheating (Hesslerová & Pokorný, 2011) and increases run-off response to precipitation (Guzha et al., 2018; Shivoga et al., 2007). The corridor is affected by local degradation (grazing, trampling and logging) as well as by catchment scale hydrological changes that strengthen the impact of local pressures.

Floodplain regeneration is dependent on flooding and on the depth of the water table (Hughes, 1988). Changes in stream hydrology and riverbed sinking affect seedling regeneration by reducing the ability of plant roots to connect to groundwater (Shafroth et al., 2000). These processes explain that when the hydrology is affected, as in our case, mesic-xeric upland taxa and exotic species tend to invade degraded floodplains (Schulz & Leininger, 1990). Hydrological changes tend to impact the riparian vegetation in an uneven fashion. Species forming the herbaceous layer, characterised by shallow roots, tend to disappear first due to the progressive disconnection from the sinking water table and are soon replaced by dry-tolerant communities. In agreement with this explanation, the composition of the vegetation encountered in quadrats shows an increase in ruderal, bushland and dry woodland herbs and grasses. The majority of these belongs to the chorotype 'Tropical East Africa'. The presence of these taxa indicates a shift to a drought-tolerant community. Conversely, large trees, provided with deep roots that allow them to adapt to sinking water tables, tend to show higher resilience at individual level and a longer 'memory' of the former floodplain. Despite floodplain degradation, riverine tree species are still present in the lower Gilgil and contribute to enhancing the taxonomic richness recorded in transects. These taxa tended to be absent in quadrats that had few tree species even as saplings, indicating a sign of low regeneration potential at population level.

5 | CONCLUSIONS

By combining quadrats and transects, our survey of the Gilgil riparian corridor recorded overall 365 identified taxa; nearly one third of them recorded only once. Based on a comparison between α and γ diversity, we estimate that this could represent roughly 2/3 of the number of species currently present.

The riparian corridor was characterised by species succession along the altitudinal gradient with spatial turnover clearly dominating the extent of community change. We noted a progressive downstream increase in tree species, but no section exhibited a local diversity hot spot characterised by high nestedness or by higher number of species.

Upstream sites included Afromontane forest taxa, indicating that streams draining the upper highlands and descending towards the dry woodland downstream form longitudinal dispersion corridors and refuges for taxa that have become rare on river terraces and beyond, where the original vegetation has been replaced by crops and exotic tree plantations. Under the present conditions, stream corridors maintain a high diversity gradient with the surrounding modified landscape and increase regional richness.

Downstream, the species gradient increased along with increasing aridity. The majority of herbs/grasses were broadly distributed taxa encroaching from the surrounding dry bush and exotics from upstream farmland. The lower meandering floodplain was characterised by greater tree diversity because of the presence of specialised riverine taxa adapted to permanent moisture conditions growing beside taxa characteristic of dry woodlands. The degraded status of the floodplain prevents the establishment of conditions that would favour the exclusion of less adapted species to the sole advantage of a truly riparian community (which would have been reflected in the predominance of the nestedness component of β diversity over species replacement).

Narrowing and degradation of the floodplain are shifting the riparian community to a more drought-tolerant one. Herbs and grasses respond more promptly to such changes. Riverine trees belong to a vestigial floodplain community characterised by few large individuals and low regeneration potential.

6 | RECOMMENDATIONS

Conservation strategies tend to focus on priority sites and priority taxa. The Gilgil riparian corridor should be preserved in toto, but with a particular attention to the ongoing degradation of the lower floodplain, where the microclimatic gradient is steeper and the riverine community is clearly distinct from the surrounding drought-tolerant vegetation. The endemic species that could warrant protection consist primarily of the forest and riverine taxa growing within the riparian corridor and rare elsewhere in the catchment. Our records did not include endangered taxa, apart from the vulnerable *Prunus africana* (Hook.f) Kalkman (IUCN Red List, CITES Annex II) that was relatively common, and *Podocarpus latifolius*

(Thunb.) R.Br. ex Mirb., which is becoming locally rare outside protected areas. It should be noted, however, that several regional endemics recorded in our samples, such as *G. kilimandscharicum*, are potentially vulnerable taxa listed as Data Deficient in the IUCN Red List, whose actual status cannot be fully evaluated because of the paucity of records.

Riparian corridors, such as the Gilgil, represent a repository of the original catchment biodiversity and a Natural Capital source of exclusive ecosystem services that cannot be generated from the surrounding dry landscape. The riparian corridor provides habitat for birds, herptiles and mammals, and it offers refuge and pasture to wildlife and cattle herds that are particularly critical during the dry season. The corridor also enhances water quality through sediment deposition and nutrient processing, and it provides direct benefits to local residents in terms of medicinal remedies and cultural values.

Future research on processes that shape diversity in riparian corridors should address factors, such as stream hydrology, that affect the regeneration potential of endemic and riparian taxa. It should do so by keeping a particular focus on keystone species in the local riparian assemblage and on species that are essential for the preservation of key ecosystem functions.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article, in the Appendices and in the Supporting Information provided as online supplementary files. Further details, including taxon-by-sample tables, can be obtained from the corresponding author.

ORCID

Nic Pacini  <https://orcid.org/0000-0002-9717-0449>

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SUPPORTING INFORMATION

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