ORIGINAL RESEARCH

Documenting the chronology of ecosystem health erosion along East African rivers

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Abstract

Pristine tropical ecosystems are currently suffering under extreme demographic pressure. This has led to habitat destruction and disturbances, an important precondition for the invasion of exotic species into pristine ecosystems, with detrimental effects on biodiversity. In this study, we analysed the chronology of land cover changes along rivers in south-eastern Kenya using historical aerial photographs and current aerial pictures taken from a drone. We assessed quantity and quality of riparian thickets along these rivers in 1961, 1980 and 2015/2016 and analysed effects of fundamental land cover changes on arthropod abundance and diversity. Our data show effects from demographic pressure by the increasing number of human settlements rising by 425% from 1961 to 2015/2016 (i.e. from 36 to 189 settlements). 58.5% of the land surface originally covered by pristine riparian forests was cleared and transformed into agricultural land. After clearance and agricultural usage it frequently became fallow land and was invaded by the exotic shrub species *Lantana camara*. While the total coverage of riparian vegetation did not change over time, its quality declined dramatically. Currently 36.6% of the cleared pristine riparian forest is covered by *L. camara* thickets, and only 22.5% of the pristine riparian forest has remained unchanged over time. This modification of the vegetation structure impacts biodiversity. The abundances of three guilds of arthropods significantly differed between pristine and *L. camara*-dominated riparian vegetation, with herbivorous arthropods and ants being more abundant in pristine than in *L. camara*-dominated vegetation. Our data show that habitat destruction and disturbance is the prerequisite for subsequent invasion by exotic plant species, having a strong effect on species composition and diversity at higher trophic levels.

Introduction

Destruction and disturbance of pristine habitats through anthropogenic activities is one of the main drivers leading to global biodiversity loss (Sala et al. 2000). Ecosystem disturbances frequently provide the prerequisite for a successful invasion and establishment of exotic species (Lake and Leishman 2004). Such invasive species may have detrimental effects on pristine biota as they frequently replace components of the original flora and fauna and may negatively affect single species and local populations, species interactions and functions (Gurevitch and Padilla 2004).

A prominent example of a successful invader in disturbed tropical ecosystems is the shrub species *Lantana camara*, originating from the West Indies (Sundaram and Hiremath 2012; Sundaram et al. 2012). Its global spread

took place during the colonial era when this plant species was introduced in many countries for fodder, energy and ornamental purposes (Day et al. 2003; Kannan et al. 2013; Urban et al. 2011). In the meanwhile, this species has become a pest, particularly in disturbed ecosystems (Duggin and Gentle 1998; Foxcroft et al. 2010; Vardien et al. 2012). In Kenya, *L. camara* was first recorded in the wild (beyond human settlements, gardens and parks) during the 1950s (Ghisalberti 2000; Richardson and Rejmanek 2011; Vardien et al. 2012). Since then, the species has naturalized across the country and invaded most regions and ecosystems, and particularly became dominant in disturbed ecosystems, for example, after clearance of riparian forests along rivers.

Riparian forests in East Africa grow along rivers and support high plant diversity as long as they are undisturbed and not dominated by any invasive exotic species. Typical indigenous plant indicators of intact riparian forests are *Commiphora samharensis*, *Croton dichogamus*, *Dombeya kirkii*, *Euphorbia bicompacta*, *Euphorbia friesiorum*, *Haplocoelum foliolosum*, *Premna oligotricha*, *Rauvolfia caffra*, *Shirakiopsis ellipticum* and *Shirakiopsis ellipticum*. Riparian forests provide important habitats for many endangered species (van Beukering and de Moel 2015), and various ecosystem services used by the local human population (Habel et al. 2015a). Demographic pressure in major parts of East Africa caused an increasing accumulation of people along rivers, with subsequent clearance of pristine riparian forests, its transformation into agricultural land and subsequent invasion and devastation by exotic species, such as *L. camara*.

In this study, we document the chronology of riparian habitat change, with the destruction of pristine riparian forests and its subsequent replacement by exotic *L. camara* thickets between 1961 (based on black-white aerial photographs taken by the British Royal Air Force) and 2015/2016 (images taken using a UAV (Unmanned Aerial Vehicle, or 'drone')). We analysed the ecological effects resulting from these fundamental changes of habitat structures on the abundance of three guilds of arthropods. Based on these data, we test the following hypotheses:

(1) Increasing demographic pressure has caused habitat destruction and disturbance and was the prerequisite for the invasion by *L. camara*.

(2) The invasion of *L. camara* caused a decrease in arthropod abundances, particularly of herbivorous species.

Material and Methods

Study region

The study region in south-eastern Kenya (1°23′S; 38°00′E) is characterized by medium to low precipitation (1079 mm annual average, divided into two distinct short rainy seasons) and moderately hot climatic conditions (mean 21.4°C) (Jaetzold et al. 2007). Thus, the region is classified as semiarid. Data were collected along two rivers, Nzeeu River and Kalundu River (Fig. 1). Most of the local people (97%) depend on subsistence agriculture with the cultivation of maize, beans, peas, mangos and pawpaw (Habel et al. 2015b). The local human population in our study region strongly increased from 1,967,301 (in 1969) to 5,668,123 inhabitants (in 2009) (KNBS, 2012). This high demographic pressure caused land-splitting and a lack of agricultural rotation (lack of fallow land stages), accelerating the reduction in soil fertility (Jaetzold et al. 2007), so that more (intact) habitats are needed to be transformed into agricultural land.

Land cover data

Historical land cover data were derived from black-white aerial photographs taken in 1961 and 1980 by the British Royal Air Force. Photographs were georeferenced in QGIS (2016a) using polynomial transformation type with nearest neighbour resampling methods in the coordinate reference system Arc 1960 / UTM zone 36S (EPSG: 21036), resulting in pixel sizes of 1.69 m in both directions. Appropriate root mean square errors and digitizing was performed afterwards.

Current land cover data were collected during September 2015 and March 2016, using an Unmanned Aerial Vehicle (DJI Phantom 2 drone), equipped with an orthogonal attached RGB digital camera GoPro HERO 4 Black (GoPro, Inc., San Mateo) mounted on a Zenmuse H3-3D gimbal. Due to limited flight time (about 18 min per mission), we divided aerial surveys into several overflights to cover 13.5 km of Nzeeu River and 17 km of Kalundu River. Flight paths of single overflights were pre-processed with QGIS to guarantee spatial overlapping of about 35–60%. Flights were performed as autopiloted stop-and-turn flights at 40 m flight altitude with 50 m spacing between loops, covering an area of 200 m stream length and 300 m riparian area on each side of the river (equalling 12 ha total area per flight, mean flight length of about 4 km). The attached digital camera was configured using medium resolution settings of seven megapixels and focal length of 21.9 mm equivalent, resulting in picture dimensions of 2250–3000 px, with aspect ratio of 3–4 reduce fish-eye distortion. Pictures were taken with a 2 sec time-lapse interval, producing an average of about 400 pictures per flight. Additionally, coloured markers were used as ground control points (GCP), which were measured using a Garmin eTrex 10 GPS device. The aerial photographs were combined afterwards with the AgiSoft Photoscan Professional software (Agisoft 2015) using medium-quality dense cloud
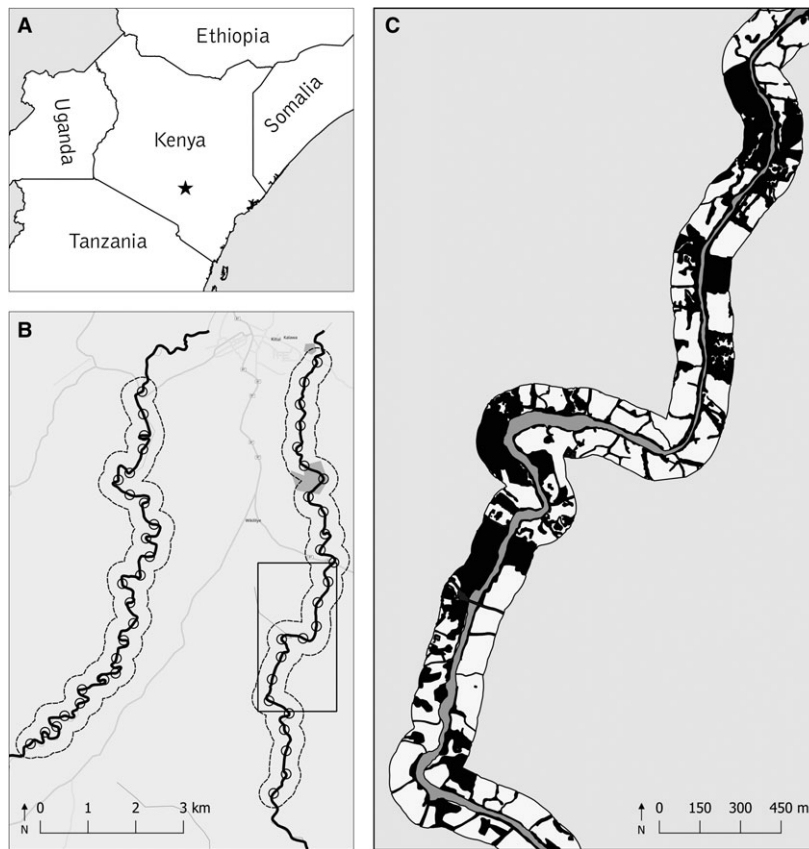
Figure 1. Study areas at three geographical scales. (A) Location of our study region in Kenya (black star). (B) Landscape scale, assessed land cover composition for 25 circles randomly set along Nzeeu River (east) and Kalundu River (west), and the detailed mapping of *L. camara* occurrence. (C) Regional scale, detailed land cover change analyses along Nzeeu River (for details see figure 2).

processing and mesh construction settings. Based on sufficient ground control points, processed imagery was exported as orthomosaic into geotif raster files with geometric accuracy below 1.97 m (1.00 m in longitudinal error, 1.38 m latitudinal error and 0.99 m altitudinal error). The tiled orthophotos were subsequently mosaicked using gdal-function merge in QGIS (GDAL 2015) and prepared for further analysis. For the quantification of land cover changes, we distinguish between the following three land cover categories: (1) riparian thickets (pristine as well as *L. camara*-dominated thickets), (2) agricultural land (1 & 2 both as polygons) and (3) human settlements (as points, with each point representing an aggregation of several houses). Digitizing was done with the software QGIS Development Team (2016a).

Land cover change

We assessed land cover changes for three spatial scales and with three methods: First, we analysed land cover changes for a 1.3 km section of Nzeeu River (Fig 1). Land cover changes were recorded within a 100 m strip on each side of this river, for three time windows: 1961, 1980 and 2015/2016. For this analysis, we also assessed all human settlements to quantify the effect of demographic

pressure. Here, the strip mapped was extended to 300 m as most people do not settle directly along the river due to periodic flooding (Fig. 2). Due to the fact that *L. camara* invaded major parts of Kenya during the 1950s and later (further details: see Introduction), we assume that all riparian vegetation detectable in the year 1961 represented intact pristine forests.

Second, to exclude potential local bias of land cover change at the above described local scale, we randomly set 50 points (25 along Nzeeu River, 25 along Kalundu River) for the years 1961 and 2015/2016 (with identical points for the two time cohorts, allowing temporal comparative analyses) (Fig 1). Each point was the centre of a 100 m radius plot (i.e. surface area 3.14 ha). These points were randomly selected using the QGIS function 'random points along line' (QGIS, 2016b). Here, we used the same land cover categories as applied in our first method.

Third, due to the fact that the proportion of *L. camara* thickets was not distinguishable from the pristine riparian forest coverage based on aerial photographs, we assessed the land cover categories for a 50 m strip along the two rivers, Nzeeu and Kalundu, with a hand-held Garmin eTrex 10 GPS device. In this third analysis, we further distinguished the land cover category 'riparian vegetation' as two sub-categories: 'pristine riparian forests' and

'disturbed riparian thickets dominated by *L. camara*' (with > 50% of the vegetation consisting of *L. camara*).

Statistical analysis

Analyses of land cover changes were calculated with QGIS and the MOLUSCE tool 3.0.11 (http://hub.qgis.org/projects/molusce). The MOLUSCE tool provides statistics for land cover class and transition matrix for the time steps to be compared. As MOLUSCE requires raster datasets as input data, we transformed the digitized land cover vector datasets into raster datasets with cell sizes of 1 m, using the QGIS conversion function. Relative errors from rasterization were calculated according to Liao and Bai (2010).

For both the local and landscape scale (steps 1 and 2, see above), we calculated land cover changes incorporating all categories. Here, we particularly focused on the conversion from pristine riparian thickets into agricultural land, the partial transformation into fallow land and subsequent succession by *L. camara*. Due to the fact that *L. camara* was first recorded in Kenya in the wild during the 1950s (Cilliers and Neser 1991), we assumed that all

riparian thickets detectable on historical aerial pictures from 1961 consist of pristine and diverse plant species composition.

We applied Land Use and Land Cover Change (LUCC) analysis to quantify the area of land cover changes. Changes were statistically validated by transition matrix, simulation and with the help of kappa statistics, which measure the agreement of two categorical datasets on a cell by cell comparison (Van Vliet et al. 2011). We considered the limitations of kappa statistics (cf. Van Vliet et al. 2011) and accordingly extended our calculations using Kappa histogram and Kappa location to clearly distinguish between quantification and location errors or agreement. Kappa histogram measures the expected agreement between two datasets based on the distribution of class sizes; Kappa location measures the maximum agreement given by the distribution of class sizes (Van Vliet et al. 2011).

Although the output of the MOLUSCE tool especially concentrates on spatial changes between time cohorts, we extended the analysis with the help of landscape metrics calculated with FRAGSTAT version 4.2 to gain insights into temporal changes of the land coverage between time
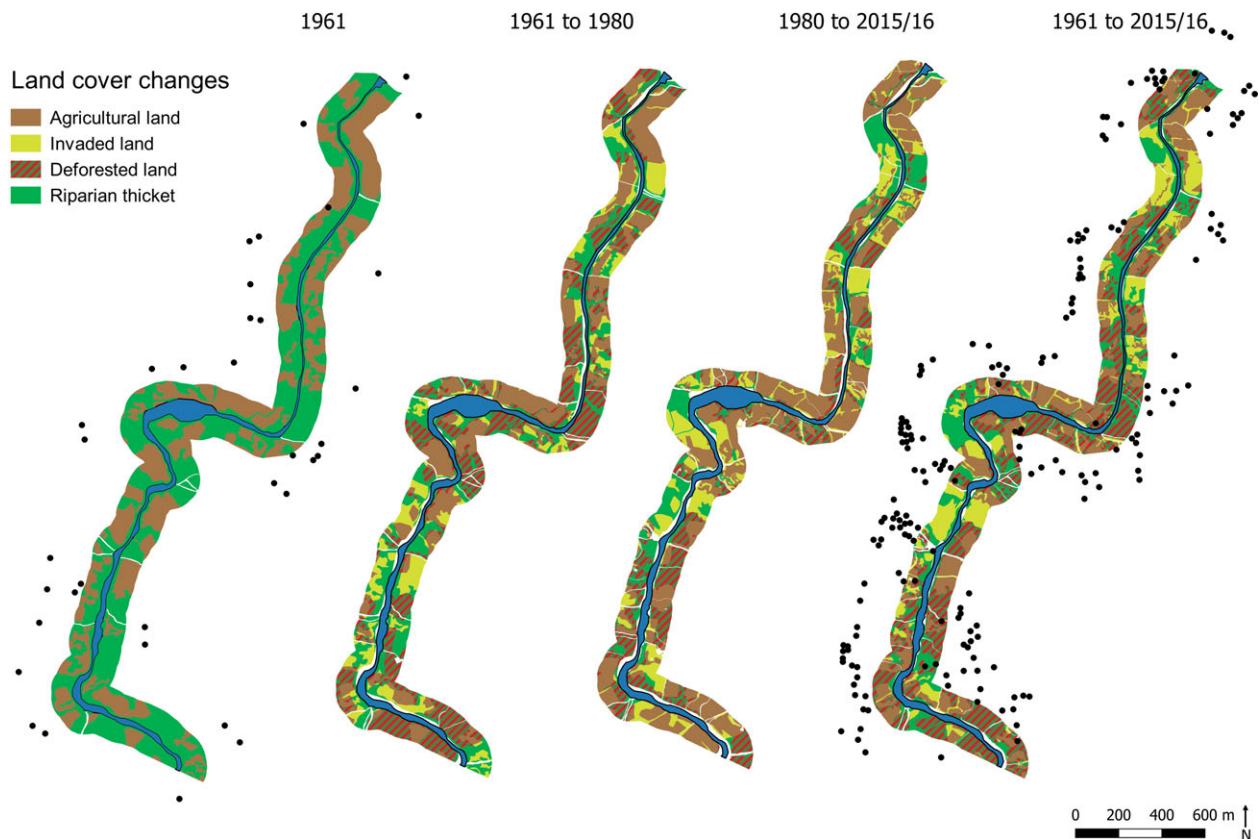
Figure 2. Land cover changes along Nzeeu River (between 1961, 1980 and 2015/2016) with the three land cover categories riparian thicket, deforested land, agricultural land, and invaded land; black dots indicate settlements.

cohorts. Here, we used an exhaustive sampling strategy for landscape scale using user-defined tiles, which were congruent with our sampling points for the LUCC analysis. At the landscape scale, we used the 25 randomly set and non-overlapping circular plots for each river (with 100 m radius) (see above). We calculated the following two indices on class and landscape level: (1) number of patches at class level and landscape level. This index provides the total number of patches for a specific landscape (i.e. the respective points of time) and classes (land cover categories). (2) Effective Mesh Size (MESH) which provides area information on fragmentation of the study area. MESH was chosen because it takes patch size and the distribution of a land cover category as well as the total landscape area into consideration (the lower limit of MESH is constrained by the cell size and is achieved when the landscape is maximally subdivided, that is, when every cell is a separate patch; MESH is maximum when the landscape consists of a single patch). Results from FRAGSTAT were post-processed using SPSS version 22 including Kruskal–Wallis H and Mann–Whitney U tests to compare the distribution of the land cover category and structural changes between the two rivers and time cohorts.

Arthropod abundance

Aggregated abundances of major arthropod orders and families were assessed using 200 pitfall traps along Nzeeu River (100 traps) and Kalundu River (100 traps). Five traps were buried in a star-wise pattern, with one at each cardinal point and a central trap, with each trap at least 5 m distant from its neighbour. Collected material from such a pitfall site (consisting of five traps) was afterwards merged and treated as coming from one site. Hence, we obtained material from 20 sites (10 sets in *L. camara*-dominated thickets, with more than 50% thicket consisting of *L. camara*, and 10 sets in pristine riparian forests, still not invaded by *L. camara*), from each of the two rivers. Each pitfall trap, with a diameter of 9 cm, was buried in the soil with its top at ground level, and filled with saturated salt solution. Traps were left in the field for 5 days (at dry weather conditions). Collection was repeated in a second round (another 5 days) under identical conditions. Sampling was conducted in March 2014 and 2015.

Arthropods were split into three groups: mainly herbivores (i.e. Lepidoptera, Homoptera, Hemiptera, Orthoptera, Cicadina), mainly predators (i.e. Arachnida, Chilopoda, Carabidae, Mantodea, Neuroptera, Staphylinidae), and ants. For each group, the average abundance between both habitat types (*L. camara*-dominated thickets vs. pristine riparian forest) was compared using

non-parametric one- and two-way PERMANOVA (Bray-Curtis dissimilarities, 5000 randomizations performed in Primer 7.0) using study year and habitat as grouping variables.

Results

Regional scale, Nzeeu River only

Data from MOLUSCE analyses show a significant change in the land cover pattern between 1961, 1980 and 2015/2016, based on the detailed land cover mapping along Nzeeu River at the regional scale (Fig. 2). 59.1% of the riparian forest cover identified for the year 1961 was transformed into agricultural land by 2015/2016. In parallel, 36.6% of agricultural land of the year 1961 became invaded by *L. camara* until 2015/2016 (Table 1). Only 34.5% of the riparian forests assessed for the year 1961 remained throughout until 2015/2016. The number of human settlements increased from 36 to 189 between 1961 and 2015/2016 (i.e. by 425%).

FRAGSTAT results indicated a severe change in the habitat configuration along Nzeeu River between 1961 and 2015/2016. The overall number of patches (including all land cover categories) increased from 138 to 218. At the level of land cover category, the number of patches (NP) for agricultural land increased from 54 to 87, for human settlement from 7 to 29, and for riparian vegetation from 62 to 88. Effective Mesh Size (MESH) decreased from 0.70 to 0.62 (Table 3). At class level, the Mann–Whitney U test revealed significant increases of the number of patches (NP) of agricultural land between 1961 and 1980, and between 1980 and 2015/2016, and for riparian vegetation between 1980 and 2015/2016. Human settlements significantly increased between 1980 and 2015/2016.

Landscape scale, Nzeeu River and Kalundu River

Landscape scale data obtained from the randomly set plots along Nzeeu River and Kalundu River showed congruent trends as revealed at the regional scale (see above). Data from MOLUSCE analyses show a significant increase in the proportion of agricultural land from 48.2% to 64.2%, while riparian vegetation coverage decreased from 44.0% to 23.8% of the total land area between 1961 and 2015/2016 (Table 2). Furthermore, 58.5% of former pristine riparian thickets became transformed into agricultural land, but 18.8% of agricultural land was covered again by thicket afterwards. Only 28.9% of the pristine riparian thickets assessed in the year 1961 existed continuously until 2015/2016. Validation showed a 95.5%

Table 1. Land cover changes between 1961, 1980 and 2015/2016 assessed along a 100 m strip along Nzeeu River, based on the following land cover categories: riparian vegetation, agricultural land, settlement.

Regional scale, Nzeeu River	1961–	1980 (1961–1980)	2015/2016 (1980–2015/16)	– (1961–2015/16)
Riparian vegetation	51.24	35.75 (−30.2%)	34.57 (−3.3%)	– (−32.5%)
Agricultural land	40.67	54.69 (+34.5%)	56.72 (+3.7%)	– (+39.5%)
Settlements	0.92	1.76 (+91.3%)	1.79 (+1.7%)	– (+94.6%)

First values indicate the area (ha). Gains and losses between time cohorts are given below as percentage in parenthesis.

correctness of the comparison, an overall Kappa value of 0.92, 0.94 for Kappa histogram, and 0.98 Kappa location. Relative rasterization error ranged from −0.0012 to 0.00056 for land cover categories (Table 3).

Data obtained from FRAGSTAT analyses indicated a severe change in the habitat configuration along the two rivers from 1961 to 2015/2016. At the landscape level, the overall number of patches (including all categories) increased from 487 to 985. At the class level, the number of patches (NP) for agricultural land increased from 185 to 196. The number of patches of riparian vegetation increased from 200 to 651. The Effective Mesh Size (MESH) decreased from 0.88 to 0.73 (Tables 3 and 4). At class level, the Mann–Whitney U test revealed significant differences of the landscape configuration between 1961 and 2015/2016 for agricultural land in terms of MESH, and for riparian vegetation in terms of NP and MESH. At land cover category (class) level, the analysis showed only significant differences between the two rivers for the agricultural land category in terms of NP in 2015/2016. Consequently, during the past five decades, total coverage of riparian vegetation strongly decreased, and the remaining patches have become strongly fragmented (Table 4).

Proportion of *L. camara*

The detailed land cover assessment of a 50 m strip along both sides of Nzeeu River and Kalundu River yielded the following proportions of land coverage: 43.8% agricultural land and 56.2% riparian vegetation. The latter land cover category consisted of 45.3% pristine riparian forests and 54.4% disturbed riparian thickets dominated by *L. camara*.

Arthropod abundance

Overall arthropod abundances across all three groups (herbivores, predators, ants) were lower in *L. camara*-dominated thickets than in pristine riparian forests (one-way PERMANOVA: P [$F_{1,259}$] < 0.01). Combining data from both study years, pristine riparian forests yielded more herbivorous arthropods (P [$F_{1,259}$] < 0.001) and ants (P [$F_{1,259}$] < 0.01), but not predators (P [$F_{1,259}$] > 0.2) (Fig. 3). Two-way PERMANOVA with study year and

Table 2. Land cover change from 1961 to 2015/2016 assessed for Nzeeu River and Kalundu River based on 25 circular plots set across the landscape along each of the two rivers. First values indicate the land cover in ha, below are given gains and losses between the two time cohorts in percentage in parenthesis.

Land cover category	Nzeeu River (1961–2015/16)	Kalundu River (1961–2015/16)	Overall (1961–2015/16)
Riparian vegetation	42.90 (−43.63)	45.07 (−48.22)	43.98 (−45.95)
Agricultural land	49.93 (+26.15)	46.45 (+40:93)	48.20 (+33.20)
Settlements	0.60 (+195.74)	0.26 (+480.00)	0.43 (+280.60)

Table 3. Rasterization errors (RE) for land cover categories.

	Year	
Land cover category	2014	1962
Agricultural land	−0.00044308	−0.00007139851
Riverbed	0.00010825	0.00047055326
Settlement	−0.00123494	0.00056181737
Riparian forest	−0.00008747	−0.00004662649

RE was calculated based on Liao and Bai (2010). Values range between 0 and 1. Positive (negative) RE indicate that the grid area after rasterization is larger (smaller) than the vector area before rasterization for the land category. The larger the absolute value, the bigger is the error.

habitat as grouping variables identified significant year × habitat interactions (P [$F_{1,258}$] < 0.05) in ant abundances. No interactions were observed for herbivores and predators (P [$F_{1,258}$] > 0.1).

Discussion

The combination of historical aerial photographs and recent aerial photographs taken from UAVs allows a temporal comparison over long time periods (cf. Yi 2017). Using UAVs is a rather novel approach in ecology and conservation biology. One of the main advantages of applying UAV systems is that they can be individually equipped with devices (sensors and cameras) (cf. Linchant et al. 2015). UAVs can achieve cloud-free images in real-time. Study-specific data can be collected with optimal

Table 4. Changes in the land cover configuration at local and landscape scale for the time windows 1961, 1980 and 2015/2016 giving details about Number of Patches (NP) and Effective Mesh Size (MESH) for overall, as well as cross-river comparison and comparison between the years 1961, 1980 and 2015/2016.

Years / Land cover category	Regional scale		Landscape scale					
	Nzeeu River		Nzeeu River		Kalundu River		Overall	
	NP	MESH	NP	MESH	NP	MESH	NP	MESH
1961	138	0.7000	261	0.2315	226	0.8529	487	0.2224
1980	144	0.6460						
2015/2016	218	0.6233	505	0.1786	479	0.7469	984	0.1827
1961								
Riparian vegetation	62	0.3881	200	0.4503	96	0.4599	200	0.4551
Settlements	7	0.0012	11	0.0036	3	0.0025	11	0.0032
Agricultural land	54	0.2128	185	0.4550	86	0.3688	185	0.4119
1980								
Riparian vegetation	54	0.2426						
Settlements	13	0.0007						
Agricultural land	63	0.3231						
2015/2016								
Riparian vegetation	88	0.2265	650	0.1015	322	0.0689	650	0.0852
Settlements	29	0.0003	67	0.0028	33	0.0018	67	0.0023
Agricultural land	87	0.3142	196	0.5644	85	0.6449	196	0.6046

camera types and flight parameters (Anderson and Gaston 2013; Salamí et al. 2014). This provides researchers with the highest flexibility. UAVs allow the collection of high-resolution data over large areas which may be too large for ground-based manual assessments, as well as access to remote areas in a time- and cost-efficient manner (Koh and Wich 2012; Chabot and Bird 2015). Compared to sub-meter high-resolution aerial imaging from manned aircraft, satellites or manual ground-based surveys, UAVs provide a very cost-effective method. Although acquisition occupies just the smaller part of the time needed until the final, ready to analyse product is obtained, the method offers the flexibility necessary to most applications compared to commercial satellite products. The latter are more accurate, but normally much more expensive, entailing the need for bulk orders with a minimal required area of several square kilometres.

Our data reveal a rapid increase of settlements and a rapid clearance of formerly interconnected riparian forests and their transformation into agricultural land. Only 34.5% of the pristine riparian vegetation has persisted until today, and most of it has become dominated by the exotic *L. camara* shrub (i.e. 80.0% along Nzeeu River). Due to the fact that *L. camara* was not yet of widespread occurrence in Kenya during 1961 (cf. Cilliers and Neser 1991), major changes in plant species composition and ecosystem quality must have taken place after clearance of pristine riparian vegetation, as documented by our chronology, which delineates the following major steps: (1) clearance of pristine riparian vegetation, (2) transformation into agricultural land, (3) change to fallow land
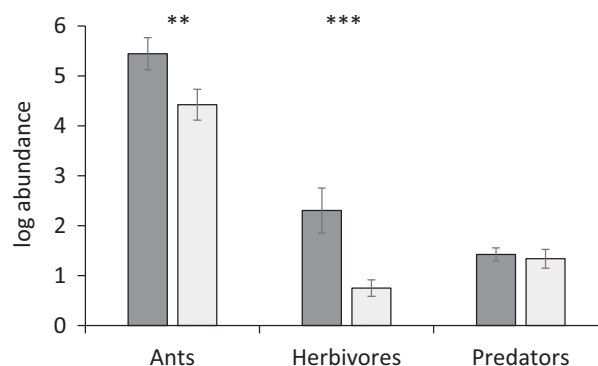
Figure 3. Arthropod abundance in pristine riparian forests (dark grey) and riparian thickets dominated by *Lantana camara* (light grey) assessed using pit fall traps along Nzeeu River and Kalundu River. Log abundances (ln-transformed mean number of individuals per site) of three major arthropod groups are given. Bonferroni-corrected significances (non-parametric one-way PERMANOVA): **$P < 0.001$, ***$P < 0.0001$.

after cessation of cultivation, (4) subsequent invasion by exotic *L. camara* (reforestation, but resulting in lower habitat quality). Lower abundance of herbivorous arthropods and ants in *L. camara*-dominated riparian thickets when compared to pristine vegetation are evidence for the negative effects resulting from this habitat change.

Tropical landscapes under pressure

Kenya is characterized by strong demographic pressure. Several studies have indicated rapid land cover changes

across the country, with severe losses of intact ecosystems and declining ecosystem health (Brink et al. 2014; Muriuki et al. 2011; Pellikka et al. 2009). Collinearities between increasing demographic pressure, transformation of intact ecosystems into agricultural land and the exploitation of natural resources (domestic use of firewood, and the production of charcoal and bricks) are underlined by our land cover change analyses. These activities caused the transformation of formerly continuous pristine riparian forests into small remnant patches, today interspersed in agricultural land (Teucher et al. 2015). Using similar analytical techniques as in our study, such trends have been observed also for other regions across Kenya, such as the Taita Hills where pristine cloud forests have been largely replaced by agricultural land and newly planted exotic forests (Pellikka et al. 2009). Also in the Chyulu Hills, human pressure has been strongly affecting pristine habitats, with a subsequent negative impact on ecosystem health (Muriuki et al. 2011).

Land cover changes and the disturbance of intact and interconnected ecosystems often go in hand with an increased vulnerability of the remaining original habitats. These conditions are often an important prerequisite for a successful invasion by exotic species, such as *L. camara* in our case (Duggin and Gentle 1998; Sharma et al. 2005). This invasion took place over major parts of Kenya during the past few decades (Day et al. 2003). The speed of invasion is assumed to be accelerated along rivers by water flux and fast seed dispersal via fruit-feeding bird species living in the riparian vegetation (Day et al. 2003; Lyons and Miller 2000). Such changes in habitat quality are assumed to negatively affect single species and entire species communities (Mortelliti et al. 2010).

Ecological effects

Our data show that declining habitat quality negatively impacts biodiversity in the riparian vegetation invaded by exotic species. A similar coherence can be observed for the cloud forest region of the Taita Hills (Pellikka et al. 2009). In general, reduced species richness has repeatedly been detected in novel ecosystems dominated by exotic plant species (Dobhal et al. 2011; Singh et al. 2014). Our data indicate that this general phenomenon also applies to the specific case of *L. camara* in south-eastern Kenya, as herbivorous arthropod abundance is higher in pristine riparian vegetation than in *L. camara* thickets. Furthermore, the decrease in ant abundance in the degraded thickets dominated by *L. camara* in comparison to the pristine sites accords with the previously recorded lower ant diversity of tropical forest plantations when compared with pristine riparian vegetation (Watt et al. 2002). Other

studies conducted in various tropical countries also indicate that *L. camara* does not provide suitable resources and even may act as an 'ecological trap' for many native animal species (Battin 2004; Delibes et al. 2001; Patten and Kelly 2010; Pulliam and Danielson 1991; Robertson and Hutto 2006). For example, Aravind et al. (2010) revealed negative effects of *L. camara* on bird diversity in India, where species diversity, species richness and abundance – particularly of habitat specialists – severely decreased once *L. camara* had become dominant. In addition to changes in habitat quality (from pristine riparian vegetation into thickets dominated by the exotic *L. camara*), we observed a severe increase in habitat fragmentation over time. This might have enhanced the negative effects on the persistence of species because local populations living in geographically isolated and small habitat patches are more prone to extinction, as indicated in various studies (Fahrig 2003).

How to deal with *L. camara*?

Various methods exist to control the invasion of *L. camara* (Broughton 2000; Bhagwat et al. 2012), such as long-time burning (Debuse and Lewis 2014; Osunkoya et al. 2013), replanting native tree species and the sub sequent shading of *L. camara* (Duggin and Gentle 1998) and the introduction of herbivorous insects that are host-specific to *L. camara* (Baars et al. 2007; Zalucki et al. 2007).

Although relatively simple means are available to strongly reduce the negative impact of *L. camara* on riparian vegetation, societal facts might largely hinder their application. While our data and other studies indicate that *L. camara* negatively influences ecosystem heterogeneity and autochthonous biodiversity, this plant species has become widely accepted by the local human populations and even has some uses, for example, for antimicrobial (Deena and Thoppil 2000; Sharma and Kumar 2009) and anti-diabetic treatments (Grover et al. 2002), as a repellent (Mng'ong'o et al. 2011), and as an anti-malarial drug (Njoroge and Bussmann 2006). This ambivalence between human usage and the necessity for elimination in the light of biodiversity conservation makes it difficult to formulate and establish clear and successful strategies for the management of this aggressive invasive plant species.

Acknowledgements

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