Rapid biodiversity assessment of myxomycetes in two regions of Kenya

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A rapid biodiversity assessment using the moist chamber culture method was carried out to determine the assemblages of myxomycetes associated with four microhabitats in two regions of Kenya. The assessment yielded a total of 60 species, of which 51 and four were new records for Kenya and Africa, respectively. Overall, 70 myxomycetes are now known from Kenya. Myxomycetes were relatively more diverse in the arid Kajiado District than in the wetter Aberdare Mountains. Species abundances and diversities of the four microhabitats were comparable in Kajiado. However, in Aberdare, the aerial litter and aerial bark microhabitats were more species-rich than the ground litter and ground bark microhabitats. Distribution of species in relation to land use/cover displayed an interesting pattern. High species diversities were recorded for montane forests, alpine zones, agricultural lands and arid lands, but diversities were moderate for seasonal forests and plantation forests. Minimal relationships existed between species richness and both elevation and pH for most microhabitats; however, significant relationships were found to exist between species abundances of aerial litter and elevation in Aberdare, and between ground bark microhabitats and pH in Kajiado. Lastly, a significant percentage of the species recorded (63 %) are frequent in the tropics while the rest are either occasional or rare.

Keywords: Slime molds, ecology, distribution, microhabitats, sampling effort, Eastern Africa.

The myxomycetes (plasmodial slime molds or myxogastrids) were first classified as fungi on the basis of the morphology of their sporocarps (Martin & Alexopoulus 1969). Moreover, myxomycetes are typically found in the same habitats as fungi. Thus, early observations of this group were mostly reported by mycologists who also treated them as fungi (e.g., Martin 1960). However, the presence of both microscopic and macroscopic amoebal trophic stages in their life cycle eventually caused mycologists to align myxomycetes with protozoan organisms (e.g., Lankester 1885). Unlike fungi, which are primarily saprotrophs, myxomycetes are phagotrophs and predators of bacteria, algae and fungi hyphae (Olive 1975, Spiegel *et al.* 2004). Feest (1987) noted that

myxomycetes are a major component of the assemblage of organisms associated with decomposition and nutrient cycling in most terrestrial ecosystems. The most recent classification of eukaryotic microorganisms places myxomycetes in the Amoebozoa (Adl *et al*. 2005, Shadwick *et al*. 2009) in the subgroup Eumycetozoa. About 880 species of myxomycetes are known to date (Hernández-Crespo & Lado 2005), which makes them one of the most rich-species subgroups in the Amoebozoa. Unlike nonfruiting amoebae, which are difficult to identify using morphological features of their cells, myxomycetes are relatively easy to identify using their sporocarp and spore morphology (Stephenson & Stempen 1994, Spiegel *et al*. 2004).

Our current knowledge of the taxonomy and ecology of myxomycetes is based primarily on studies from north temperate regions of the world (Martin & Alexopoulos 1969, Nannenga-Bremekamp 1991, Stephenson 2003). Recent initiatives that have attempted to collect both taxonomic and ecological data have helped to increase the body of information on myxomycetes, especially in the less studied regions of the Neotropics (Ogata *et al*. 1996, Stephenson *et al*. 2004, Rojas & Stephenson 2007, 2008, Estrada-Torres *et al*. 2009), arid regions of Eastern Europe (Novozhilov *et al*. 2006, Novozhilov & Schnittler 2008), Asia (Stephenson *et al*. 2000, Tran *et al*. 2006, 2008), South America (Lado *et al*. 2007), New Zealand (Stephenson 2003) and Ascension Island in the South Atlantic (Stephenson 2009). At the moment, data obtained from these regions have provided evidence of species distribution patterns that would seem worthwhile investigating further, particularly in less studied regions. For example, the idea that temperate forests are more species-rich than tropical forests has been questioned (Ing 1994, Lado & Wrigley de Basanta 2008). Unlike the situation in temperate forests, where myxomycetes are abundant on ground substrates, the few studies that have considered a wide range of substrates in tropical forests have reported more species on aerial than on ground substrates (Schnittler *et al*. 2002). In addition, results obtained from several different arid regions indicate that the substrates present support diverse assemblages of myxomycetes (e.g., Lado *et al*. 2003, 2007; Novozhilov & Schnittler 2008, Estrada-Torres *et al*. 2009). Previously ignored anthropogenically modified habitats (e.g., croplands) also have been found to support myxomycetes (Tran *et al*. 2008).

Studies of the taxonomy and ecology of myxomycetes in Africa are still in their infancy. In the past, most reports of myxomycetes in Africa came from foreign mycologists who were primarily interested in fungi (Farquharson 1916, Patouillard 1928, Wiehe 1948). Moreover, the majority of these reports were anecdotal and the lists of species compiled consisted mostly of only a few species (e.g., Kost 2002). The few extensive surveys carried out in Africa have yielded more impressive species lists. For instance, between 1988 and 1995, Ukkola (1998) reported 133 species from Tanzania, and this is the highest total of spe-

cies reported to date from a single country in Africa. Other countries for which significant numbers of myxomycetes records exist include Morocco (123 species), South Africa (107), Algeria (79), Nigeria (77), Angola (72), Seychelles (56), Liberia (52) and Malawi (47). A review of myxomycete occurrences in Africa showed that records of myxomycetes exist for 32 countries and territories but that there are none for 26 countries (Ndiritu *et al.* 2009a).

Research on myxomycetes remains poorly funded in most regions of the world. However, research experiences and observations derived from previous studies can be useful in designing future studies. Spiegel *et al.* (2004) noted that a complete sampling of myxomycetes in an area should consider both field collections and those obtained from moist chambers cultures, and all substrates on which myxomycetes are known to occur must be adequately surveyed. Meanwhile, depending on the study objectives either of the two methods can be used, as both methods have been reported to complement each other in a number of studies (Schnittler *et al.* 2002, Tran *et al.* 2008). The fact that it is possible to assess a particular sampling effort using a variety of estimators offers the unique potential to design a cost-effective sampling strategy to generate an adequate body of data that is comparable with those obtained in other studies (e.g., Unterseher *et al.* 2008). For the most part, the sporocarps of myxomycetes occur on certain clearly defined substrates, including aerial litter (dead but still attached plant parts), ground litter, dead fragments of bark on the ground, decaying wood, soil and dung. Each of these can be referred to individually as a microhabitat (*sensu* Stephenson 1989). Evidence from numerous studies indicates that each microhabitat tends to support a unique myxomycete community.

In Kenya, considerable biodiversity data exist for plants, animals and fungi for major ecosystems such as forests, woodlands, shrublands and grasslands (Beentje 1994, WRI 2007). However, only few records exist for eukaryotic microorganisms, including myxomycetes (http://www.gbif.org/). In order to increase our baseline knowledge of myxomycete biodiversity in Kenya, rapid assessment surveys were carried out in two regions with contrasting ecological-climatic types. These were the Aberdare Mountain region and the Kajiado District. The Aberdare Mountain region is mountainous and characterized by several land use/cover types, including forests (plantation, xeromorphic, seasonal and wet), shrubland, subalpine, alpine, pasturelands and croplands. The Kajiado District is a semiarid region in which the predominant vegetation consists of acacia shrublands and woodlands, which are used primarily for grazing by livestock and wildlife. The specific objectives of these two surveys were (1) to determine the composition of the assemblages of myxomycetes associated with the four main microhabitats in the different land use/cover types; (2) to assess the sampling effort involved in the surveys; (3) to describe community struc-

ture in the different microhabitats; and (4) to compare our results with other studies carried out in other regions of the world.

Materials and Methods

Study areas

The two surveys were carried out in the Aberdare Mountain region and the Kajiado District (Figure 1). The Aberdare Mountains are situated in central Kenya, along the equator, between latitude 0.0º and 0º 43' S, longitude 36º 3'and 37º 0' E and elevations range from 1700 to 4000 m above sea level. The region is characterized by deeply dissected topography, sloping gently to the east while the western side drops steeply along an impressive fault escarpment towards the Rift Valley. The climate is bimodal, with wet seasons occurring from April to May and October to December. The distribution of rainfall varies seasonally as well as spatially and temporally and contrasts with temperature, which is usually elevation dependent. Frosts are common from 2470 m upwards and the lowest temperatures occur in July and August (Braun 1986). Annual rainfall reaches 2600 mm on the southeastern side and drops to less than 900 mm on the northern and southwestern lee slopes areas.

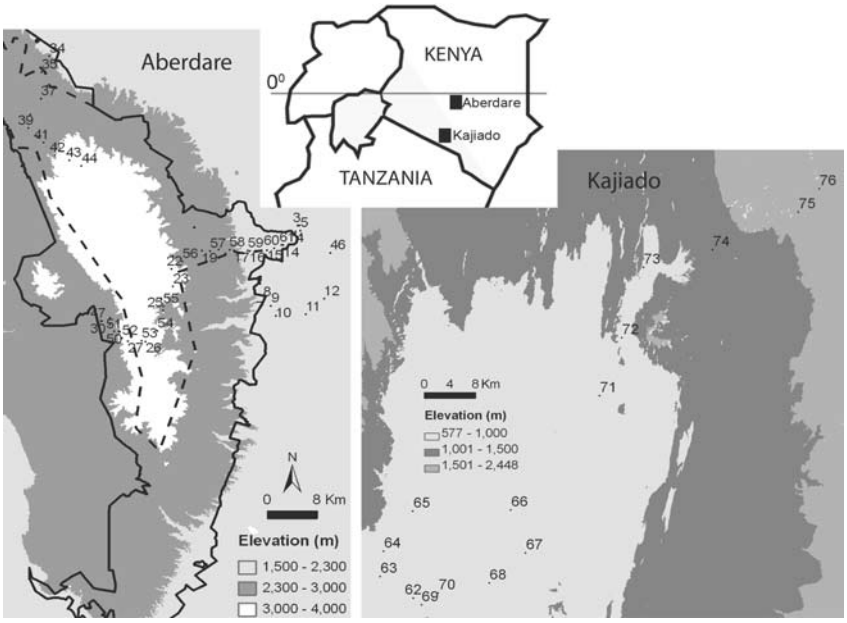

Fig. 1. – A map of Kenya showing the locations of the two study areas of Aberdare and Kajiado. Shown in the Aberdare region are study sites (1-61) and areas within the national park and forest reserve that are marked by dashed and solid lines, respectively. In both areas, study sites were established along an elevation gradient.

The vegetation types of the Aberdare Mountain region have been described by several authors (Fries & Fries 1948, Hedberg 1951, Agnew 1985). Schmitt (1991) observed that vegetation types in the region are complex; however, using an elevational gradient and floristic criteria he proposed four formation classes consisting of 34 communities. The four classes consist of forests (with 17 communities), grassland and secondary bushland (between submontane forest and subalpine zones with 11 communities), bush- and shrubland (6 communities) and grasslands (found in subalpine and alpine zones and represented by 10 communities). Meanwhile, the present vegetation cover in the region is the result of natural succession (Agnew 1985) as well as past and current human activities (i.e. fire, logging, cultivation, burning) and the activities of large herbivores (i.e., grazing, debarking) (Schmitt 1991, Lambrechts *et al*. 2003). The structure and composition of the vegetation suggest that most forests are secondary, and vegetation regeneration continues to be impeded by the large numbers of herbivores, particularly in lower elevation zones (1900 m – 2300 m). A large portion (2500 km^2) of the Aberdare Mountain region is protected under park and forest management while the other portion is under agricultural use. Pristine or at least little-disturbed forests and habitats are found only in the park's higher elevation zones (2300 m – 4000 m). The park and forest reserves are surrounded by forest plantations and agriculture lands. Human activities are minimal in the park and natural forest reserves and moderate in forest plantations, which mostly consist of *Eucalyptus* spp., *Cupressus* spp., *Pinus* spp., and *Grevelia robusta*. Large and small mixed agriculture is intensively practiced outside the park and the crops grown include coffee, tea, maize, beans and various vegetables.

The Kajiado District is located in southern Kenya, on the floor of the Eastern Rift Valley, and borders Tanzania to the south (Figure 1). The area falls between latitudes 1° 10' S and 3° 01' S and longitudes 36° 05' E and 37° 55' E, with ranges in elevation from 600 m to 2300 m. The climate of the region is essentially semi-arid. The annual rainfall is 765 mm and varies with elevation. The distribution of rainfall is bimodal and wet seasons occur in March to May and October to December. The region has consistently high ambient temperatures (26 °C - 33 °C) and high potential evapotranspiration, which ranges from 1700 mm to 2500 mm per year. The vegetation of the Magadi area consists of Acacia bushland and woodland, although riverine forests and areas of grassland occur along the Ewaso Ngiro River.

Study sites and substrates collection

A total of 76 study sites (each 20 m × 20 m) were established in both regions (Figure 1). In the Aberdare Mountain region, sites 47 to 61 and 1 to 46 were sampled in July and August of 2004 and 2005, respec-

tively. For Kajiado, samples were collected from sites 62 to 76 in August 2005. Samples were collected along an elevation gradient and in areas characterized by different land use/cover regimes (i.e., natural and human disturbed) and vegetation types (i.e., arid lands, crop lands, pastures, bushland, plantation forests, seasonal and montane forests, subalpine and alpine communities) (Table 1). In all cases sampling followed roads and sites were established approximately 50 m from the roads to minimize edge effects.

Tab. 1. – Distribution of study sites in the six major land use/cover surveyed.

Land use/cover	Number of sites and localities	Elevation (m)
Arid lands	15 sites (62–76)	600–2300
Agricultural lands	18 sites (1–5, 7–12, 35–39, 45)	1830–2300
Plantation forests	6 sites (6, 30, 33, 46–48)	1785–2600
Seasonal forests	9 sites (13–15, 31, 59–62)	1915–2085
Montane forests	17 sites (16–21, 27–29, 34, 40–42, 49, 50, 57, 58)	2230–3000
Subalpine/alpine communities	13 sites (22–26, 43, 44, 51–56)	2970–3400

Sampling methods followed those described by Spiegel *et al.* (2004) and the Eumycetozoan Project website (http://slimemold.uark.edu). For this study myxomycetes were primarly obtained using the moist chamber culture method because the sampling period was short (less than one month) and the main goal of the survey was to cover a large area, which made it unrealistic to include field collections methods that require a longer survey period. All of the different types of substrates known to yield myxomycetes were collected if they were present at a particular site, except for decaying wood and herbivore dung. Whereas myxomycetes strongly associated with decaying wood rarely develop in laboratory (Schnittler *et al.* 2002), herbivore dung was not common in most sites established and thus was not included during this survey. Substrates were classified to a particular microhabitat based on their type and where they were collected. As already noted, by microhabitat we refer to a unique refined fraction of the total habitat (*sensu* Stephenson 1989). The four microhabitats considered in the present study were aerial litter and aerial bark (defined as occurring above the ground surface) along with ground litter and ground bark (defined as occurring on the surface of the ground surface). Samples representing the ground litter and ground bark microhabitats were plant primary tissues and fragments of bark, respectively, occurring on the ground surface. At each study site a composite sample (approximately 200 g) consisting of all plant substrates present for each of the four microhabitat category was collected separately. Samples were placed in paper bags, air-dried, and shipped to the University of Arkansas in the United States. Numbers of samples collected for each

microhabitat in both regions are given in Table 2. During sampling, notes were made in each study site to describe the general land use/cover type. Elevation and geographical coordinates were determined using a global positioning system (GPS) receiver and topographic maps.

Laboratory analyses and species identification

There were no myxomycete sporocarps encountered in the field. All myxomycete collections considered here were obtained exclusively through the use of moist chamber cultures as described by Stephenson & Stempen (1994). The moist chambers consisted of Petri dishes (15 cm diam.) lined with filter paper and containing the sample material. Depending on the amount of material available per sample, one to four moist chamber cultures were prepared. Sterilized distilled water was added to each culture to flood it; 24 h later pH was determined, and then excess water was decanted. The cultures were incubated under ambient light and at room temperature (19–22 °C) for ca. 120 days and checked for the presence of myxomycetes on five occasions (days 4–7, 20–24, 40–45, 70–75, and 110–120). For each moist chamber, only one collection per species was made, and multiple occurrences of a particular species in the same moist chamber were considered as one collection or record (e.g., Stephenson 1989). The total number of sporocarps per species encountered during the entire incubation period was quantified as described by Nozozhilov *et al*. (2000). Vouchers of the species (or collections) were deposited in the mycological herbarium (UARKM) of the University of Arkansas, but it is anticipated that most of these specimens will be sent to the National Museums of Kenya in the future. Species identifications were based primarily on morphological features and were made with the use of several published articles and standard monographs (e.g., Martin & Alexopoulos 1969, Stephenson 2003). Nomenclature follows that proposed by Hernández–Crespo & Lado (2005) except for *Stemonitis fusca* var. *nigrescens* (Rex) Torrend which was recognized as distinct from *Stemonitis fusca*.

Data analyses

The completeness of our sampling effort for each of the four microhabitats was assessed with the use of the estimator of incidence (ICE), abundance-based coverage (ACE) and CHAO2 (Colwell, 2006). These three estimators are conservative and appropriate for assessing myxomycete richness (e.g., Unterseher *et al*. 2008). The sampling effort (or the percentage of completeness) for each microhabitat was determined by dividing the actual number of species recorded by the average number of species estimated by all three of the estimators. Community structure was described by the species abundance distribution measures of species diversity (using the Shannon index, Shannon &

Weaver 1949), evenness (Shannon evenness, Pielou 1975), dominance (Simpson index, Simpson 1949) as well as species rank/abundance plot, which, shows the commonness and rarity of species (Magurran 2004). The relative frequency of each species was assessed using abundance indices (Stephenson 1993). The abundance indices are "rare" (for species represented by < 0.5 % of total number of species records for that particular microhabitat in a region), "occasional" (> 0.5 % but < 1.5 %), "common" (> 1.5 % but < 3 %) and "abundant" (for species represented by > 3 %). Communities from different microhabitats were compared using sample-based rarefaction curves (Coleman *et al.* 1982), similarities indices of Morisita and Horn overlap (Towner 1999). Morisita's index is based on the logic of the Simpson diversity index, whereas the Horn's index is based on the logic of the ShannonWiener index. Both indices are based upon the species identity and their abundances, with values ranging from 0 to 1, with the latter indicating an increasing degree of similarity between the two communities being compared. In addition species distribution patterns among the four microhabitats and six landuse/cover types were examined using Detrended Correspondence Analysis (DCA) (ter Braak & Šmilauer 1999). During DCA, rare species of myxomycetes (i.e. those that were recorded from only a single site) were excluded. The relationship between species assemblages with elevation and pH was determined by linear regression analyses. Species richness and abundances were treated as dependent variables while pH and elevation were selected as the independent variables. Prior to regression analyses, the data were log-transformed to meet the criteria of normality.

Results

Study completeness

A total of 60 species was recorded, consisting of 46 and 38 species in the Aberdare Mountain region and Kajiado District, respectively (Table 2). Fifty-one of these were the first records for Kenya and four had not been reported previously from Africa. During the 2004 and 2005 surveys, 21 and 40 species, respectively, were recorded in the Aberdare Mountain region. Although the numbers of samples collected from each of the ten microhabitats were different, assessment of species data indicated that our sampling effort was fair to moderately adequate. In all cases species richness estimated by ACE was low and was not considered in the assessment of the sampling effort. Although the values of sampling effort for the 2004 survey were high, careful consideration of the data generated by the ICE and CHAO2 estimators, the rarefaction curves and comparison with data from 2005 collected in the same area suggested that the survey was inadequate and unreliable (Table 2, Figure 2). Similarly, the sampling efforts for the 2005 survey was low for aerial bark and ground bark in the Aberdare Moun-

tain region and on ground litter and bark microhabitats in Kajiado District. Although data for some of the under-surveyed microhabitats were considered during the regression and community similarities analyses, care was taken during the interpretation of these data. Meanwhile, a sampling effort of 25 to 30 samples of aerial litter and ground litter collected in Aberdare Mountain region during the months of July and August in 2005 were determined to be 70 % complete (with 29 species) and 33 % complete (17 species), respectively. For the other microhabitats, numbers of samples collected were inadequate and no serious predictions could be made; however, it should be noted that most of the widespread and common species were recovered in all of the microhabitats surveyed (Figure 2B and 2C).

Myxomycete abundance and diversity

An examination of the data for species per sample, records and sporocarps per moist chamber showed some consistent and contrasting patterns of species abundance and distribution between the two regions (Table 2). Both mean species per sample and records per moist chamber were high in all microhabitats from the Kajiado District (with ranges from 1.0 to 1.8 species and 1.4 to 2.8 records) when compared to those of Aberdare Mountain region (with ranges from 0.5 to 0.9 species and 0.6 to 1.3 records). Most of moist chamber cultures were positive (80 % to 100 %), meaning they yielded sporocarps and/or showed some evidence of the presence of plasmodia. In both regions, species diversity, evenness and dominance were comparable. For the Aberdare Mountain region, species abundances were high on the aerial litter and aerial bark microhabitats, moderate on ground litter and low on ground bark (Figure 3A). Unlike the case in the Aberdare Mountain region, species abundances were high on ground litter and moderate on aerial litter, ground bark and aerial bark in the Kajiado District. Further comparisons of the assemblages of myxomycetes from the various microhabitats with the use of rarefaction indices showed that species richness was high on aerial bark in the Kajiado District and on aerial litter in the Aberdare Mountain region (Figure 3B). Numbers of species were moderate on ground litter and aerial bark in the Aberdare Mountain region as well as on aerial litter, ground litter and ground bark in the Kajiado District.

Ecology and distribution

Community similarity results obtained with the Morisita's and Horn's indices suggest that occurrences of myxomycetes were to a certain degree influenced by macrohabitats and microhabitats (Table 3). Species assemblages seemed less similar between the two regions and in some instances higher similarity values were observed among related substrate types (e.g., bark or litter) in the same region. This dis-

Tab. 2. – Species abundance[a], diversity and relative abundance[b] (values in italics) indices of myxomycetes recorded in Aberdare and Kajiado. Also provided are recorded and estimated species richness. Acronyms refer to microhabitats: AL, aerial litter; GL ground litter; AB, aerial bark; GB, ground bark; (–) absent; MC, moist chambers. Species are arranged from the most to the least abundant.

	Aberdare Mountain						Kajiado District				AI[c]
	2004		2005				2005				
	AL	GL	AL	AB	GL	GB	AL	AB	GL	GB	
Samples	**15**	**15**	**46**	**19**	**46**	**23**	**15**	**13**	**15**	**13**	
Moist chambers	**30**	**30**	**145**	**39**	**158**	**42**	**34**	**26**	**41**	**19**	
Species											
Perichaena depressa	12.7	0.1	49.0	71.2	20.9	25.4	37.5	52.2	74.0	62.8	A
	14.0	*4.8*	*15.4*	*27.8*	*15.1*	*34.8*	*21.1*	*16.0*	*20.0*	*20.8*	
Arcyria cinerea	–	–	15.2	5.6	5.6	0.7	20.5	6.6	6.4	5.1	A
			9.8	*8.3*	*12.3*	*4.3*	*15.8*	*6.0*	*5.0*	*8.3*	
Didymium difforme	16.6	15.3	3.0	0.6	1.5	–	12.1	–	–	–	A
	20.0	*28.6*	*8.1*	*5.6*	*8.2*		*2.6*				
Perichaena chrysosperma[d]	1.8	–	6.2	1.4	7.7	3.4	1.9	8.0	5.8	23.3	A
	4.0		*3.3*	*5.6*	*6.6*	*13.0*	*2.6*	*10.0*	*5.0*	16.7	
Physarum didermoides	5.0	2.3	8.3	13.8	0.6	13.6	–	25.8	32.8	–	A
	4.0	*4.8*	*6.5*	*5.6*	*2.7*	*8.7*		*6.0*	*10.0*		
Diderma effusum	3.7	3.8	18.4	6.3	35.7	2.2	–	–	1.8	0.8	A
	6.0	*9.5*	*5.7*	*2.8*	*12.3*	*8.7*			*2.5*	*4.2*	
Physarum pusillum	0.1	2.8	1.5	–	1.3	2.0	2.7	0.8	7.6	7.5	A
	2.0	*14.3*	*2.4*		*1.4*	*8.7*	*10.5*	*2.0*	*10.0*	*8.3*	
Didymium squamulosum	12.0	5.1	3.7	–	2.8	0.2	–	–	2.5	–	A
	8.0	*14.3*	*3.3*		*5.5*	*4.3*			*2.5*		
Perichaena vermicularis	–	–	1.0	–	–	0.3	22.9	5.8	2.5	–	A
			2.4			*4.3*	*7.9*	*6.0*	*7.5*		
Physarum compressum	4.7	0.3	16.9	4.4	0.1	–	8.3	6.7	–	–	A
	4.0	*4.8*	5.7	*8.3*	*1.4*		*2.6*	*2.0*			
P. echinosporum	3.1	–	7.4	–	6.3	–	–	–	–	0.4	C
	10.0		*4.1*		*5.5*					*4.2*	
Diderma subdictyospermum	3.7	–	19.4	2.0	4.1	10.0	–	–	–	1.9	C
	4.0		*4.1*	*5.6*	*4.1*	*4.3*				*4.2*	
Physarum cinereum	–	–	3.2	–	0.4	–	15.8	16.3	10.9	16.0	C
			4.9		*2.7*		*5.3*	*4.0*	*5.0*	*4.2*	
Comatricha laxa	–	–	–	–	–	–	0.5	2.1	2.5	1.0	C
							10.5	*6.0*	*2.5*	*4.2*	
Didymium iridis	13.8	–	1.1	–	2.1	–	–	–	–	–	C
	10.0		*2.4*		*2.7*						
Physarum straminipes[e]	–	0.9	0.1	0.4	0.4	–	–	2.6	2.8	–	C
		4.8	*0.8*	*2.8*	2.7			*4.0*	*2.5*		
Stemonitis fusca var. *nigrescens*	–	–	4.1	0.6	1.0	0.3	17.5	–	3.2	–	C
			3.3	*2.8*	*1.4*	*4.3*	*5.3*		*2.5*		
Didymium anellus	9.2	–	–	–	–	–	0.4	0.5	0.4	5.0	C
	2.0						*2.6*	*2.0*	*2.5*	*8.3*	
D. saturnus[e]	–	–	5.0	0.9	–	–	–	–	2.5	–	O
			3.3	*2.8*					*2.5*		
Comatricha tenerrima[d]	–	–	–	–	–	–	0.2	1.0	1.9	–	O
							2.6	*6.0*	*2.5*		

Tab. 2. – continued.

	Aberdare Mountain						Kajiado District				AI[c]
	2004		2005				2005				
	AL	GL	AL	AB	GL	GB	AL	AB	GL	GB	
Macbrideola oblonga[e]	–	–	–	–	–	–	–	1.2 *6.0*	–	15.4 *4.2*	O
Didymium nigripes	–	–	0.4 *0.8*	–	1.3 *1.4*	–	–	–	–	–	O
Comatricha elegans	–	14.4 *4.8*	–	–	–	–	–	1.0 *2.0*	0.3 *2.5*	–	O
Fuligo cinerea	–	–	0.4 *0.8*	0.1 *2.8*	–	–	–	1.7 *2.0*	–	–	R
Collaria arcyrionema	–	–	1.3 *0.8*	2.2 *2.8*	–	–	–	–	–	–	R
Physarum bivalve	–	–	1.7 *1.6*	–	0.6 *1.4*	–	–	–	1.0 *2.5*	–	R
Physarum sp. *A*	–	–	0.3 *0.8*	–		–	–	–	–	–	R
Badhamia macrocarpa	–	–	–	–	–	–	–	0.9 *4.0*	–	1.1 *4.2*	R
B. panicea	–	–	–	–	1.9 *1.4*	–	–	–	2.5 *2.5*	–	R
Calomyxa mettalica	–	–	–	–	–	–	–	0.5 *4.0*	–	–	R
Didymium clavus	0.5 *2.0*	–	0.2 *0.8*	–	–	–	–	–	–	–	R
D. minus[d]	5.5 *4.0*	–	0.3 *0.8*	–	–	–	–	–	–	–	R
Lamproderma scintillans	–	1.5 *4.8*	0.8 *0.8*	–	0.4 *1.4*	–	–	–	–	–	R
Physarum serpula[d]	–	–	–	–	–	–	1.0 *5.3*	2.9 *4.0*	–	–	R
Stemonitis flavogineta	–	–	–	–	0.2 *1.4*	–	–	–	0.5 *2.5*	–	R
Calomyxa sp.	–	–	4.9 *0.8*	12.4 *5.6*	–	–	–	–	–	–	R
Comatricha pulchella	–	–	–	–	–	0.1 *4.3*	–	0.2 *2.0*	–	–	R
Craterium aureum	–	0.4 *4.8*	0.3 *0.8*	–	–	–	–	–	–	–	R
C. concinnum	–	–	–	–	15.4 *1.4*	12.8 *4.3*	–	–	–	–	R
Didymium bahiense	0.6 *4.0*	–	–	–	–	–	–	–	–	–	R
Hemitrichia serpula	–	–	1.8 *1.6*	–	–	–	–	–	–	–	R
Perichaena dictyonema	–	–	2.0 *1.6*	–	–	–	–	–	–	–	R
Physarum melleum	–	–	4.2 *1.6*	–	–	–	–	–	–	–	R
Stemonitis herbatica	–	–	–	–	–	–	8.3 *2.6*	–	–	3.0 *4.2*	R

Tab. 2. – continued.

	Aberdare Mountain						Kajiado District				AI[c]
	2004		2005				2005				
	AL	GL	AL	AB	GL	GB	AL	AB	GL	GB	
Arcyria denudata[d]	–	–	–	–	–	–	–	0.3 *2.0*	–	–	R
A. obvelata	–	–	2.7 *0.8*	–	–	–	–	–	–	–	R
A. pomiformis	–	–	–	–	–	–	–	0.5 *2.0*	–	–	R
Badhamaia melanospora	–	–	–	0.4 *2.8*	–	–	–	–	–	–	R
Stemonaria longa	–	–	–	3.8 *2.8*	–	–	–	–	–	–	R
Craterium minutum	–	–	–	–	–	–	–	–	0.2 *2.5*	–	R
Cribraria oregana	–	–	–	–	0.6 *1.4*	–	–	–	–	–	R
Diachea leucopodia	–	–	–	–	0.4 *1.4*	–	–	–	–	–	R
Diderma chrondrioderma	–	–	–	–	–	–	–	0.2 *2.0*	–	–	R
Diderma hemisphaericum[d]	0.2 *2.0*	–	–	–	–	–	–	–	–	–	R
Didymium ochroideum[e]	–	–	–	–	–	–	0.4 *2.6*	–	–	–	R
Perichaena corticalis	–	–	–	18.1 *2.8*	–	–	–	–	–	–	R
P. quadrata	–	–	–	0.8 *2.8*	–	–	–	–	–	–	R
Physarum bogoriense	–	–	–	–	1.4 *1.4*	–	–	–	–	–	R
P. crateriforme	–	–	–	–	–	–	–	0.7 *2.0*	–	–	R
Physarum sp. *B*	–	–	–	–	–	–	–	–	0.7 *5.0*	0.2 *4.2*	R
Trichia favoginea	–	–	–	–	9.7 *1.4*	–	–	–	–	–	R
Positive MC (%)	100	90	92	90	86	93	79	92	83	89	
Number of records	64	26	169	50	94	29	50	72	60	27	
Recorded species	16	15	31	18	26	12	15	23	21	14	
Species per sample	1.1	1.0	0.7	0.9	0.6	0.5	1.0	1.8	1.4	1.1	
Records per MC	2.1	0.9	1.2	1.3	0.6	0.7	1.5	2.8	1.5	1.4	
Mean pH	6.6	6.7	6.9	6.9	7.3	7.0	6.4	6.8	6.8	6.8	
Minimum	5.2	7.1	7.7	7.7	8.2	7.5	7.0	7.1	7.3	5.4	
Maximum	7.5	5.8	6.0	4.3	5.2	5.2	5.3	5.4	5.6	7.1	
Shannon index *(H')*	2.36	1.54	2.38	1.72	2.09	1.62	2.14	1.92	1.82	1.72	
Shan. evenness *(J')*	0.72	0.69	0.71	0.59	0.70	0.65	0.72	0.61	0.60	0.65	
Simpson index *(D)*	0.08	0.15	0.08	0.22	0.10	0.16	0.12	0.15	0.20	0.21	
ACE	15	11	31	18	26	12	15	23	21	12	

Tab. 2. – continued.

	Aberdare Mountain						Kajiado District				AI[c]
	2004		2005				2005				
	AL	GL	AL	AB	GL	GB	AL	AB	GL	GB	
ICE	21	25	41	43	52	33	24	42	52	36	
CHAO2	22	35	41	34	51	26	24	29	53	29	
Sampling effort (%)[f]	74	50	76	47	50	41	63	65	40	43	

[a] Sporocarps per species in a sample (sporocarps per moist chamber, diam. 15 cm).
[b] Species records divided by total species records for that particular microhabitat. Values obtained are similar to abundance indices by Stephenson *et al.* (1993), where a species is regard as abundant if represented by (> 3 % of all records for that particular microhabitat), common (1.5 % to 3 %), occasional (0.5 % to 1.5%) and rare (< 0.5 %).
[c] AI is overall species abundance indices of a species from all microhabitats in both regions. Abbreviations represent: A, abundant; C, common; O, occasional; and R, rare.
[d] Species reported earlier for Kenya; 52 species without superscript ([c]) are first records for Kenya.
[e] Species that are new records for Africa.
[f] Sampling effort was the number of species recorded divided by the mean value of estimated species richness of incidence–based coverage estimator (ICE) and CHAO2. Note that the abundance coverage estimator (ACE), underestimated species richness and thus was not used to determine the percentage of sampling effort.

tribution pattern was somehow captured by the DCA which ordered species assemblages from Kajiado and Aberdare regions into two separate groups (Figure 4). *Perichaena depressa, P. chrysosperma* and *Arcyria cinerea* were the most widespread and abundant species and were the only species found in all microhabitats in both regions. Species that were abundant only in one or more microhabitats in Aberdare region included *Comatricha tenerrima, Diderma effusum, D. subdictyospermum, Didymium difforme, D. iridis, D. squamulosum, D. saturnus*, *Physarum compressum* and *P. echinosporum*, whereas *Comatricha laxa, Didymium anellus, Perichaena vermicularis* and *Physarum straminipes* were frequent in the Kajiado District. *Physarum didermoides,* and *P. pusillum* were abundant in one or more microhabitats in both regions. Meanwhile, all the other forty-six species recorded were either common, occasional or rare in one or more microhabitats in one or both regions

Numbers of samples obtained from various land use/cover classes were different; however, data obtained in well-sampled classes allowed us to draw some preliminary conclusions (Table 4; Figure 5A and 5B). On aerial litter, species abundances and richness were high for montane forest and subalpine/alpine, moderate for arid lands and low for seasonal and plantation forests. Ground litter was similar to aerial litter, with species richness and abundance high for subalpine/

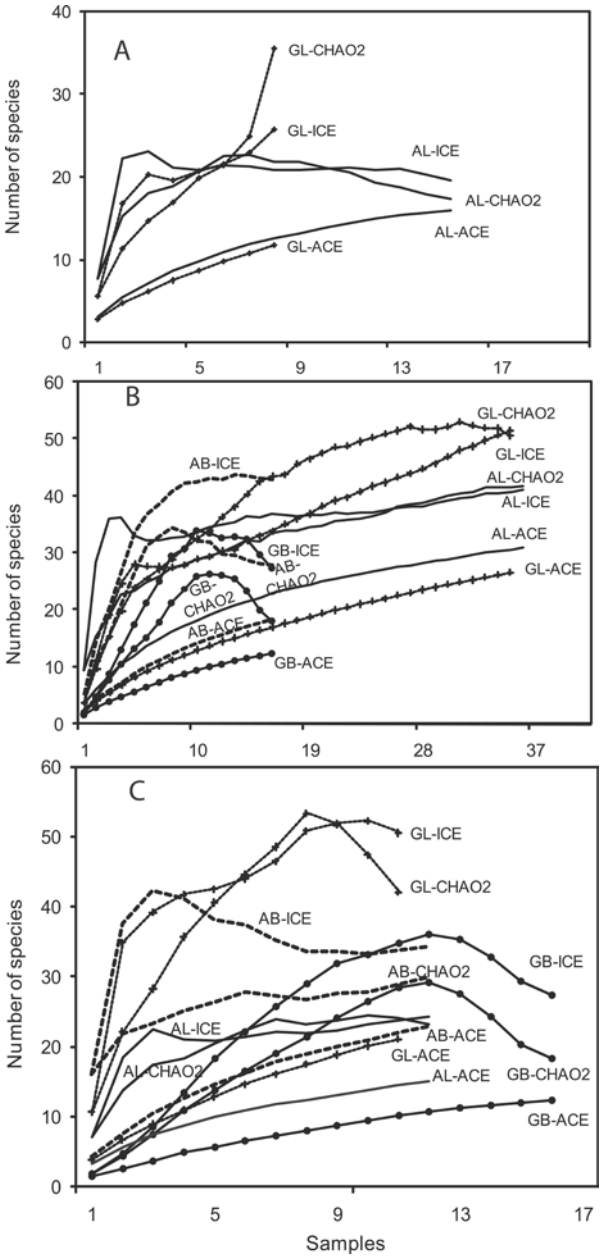

Fig. 2. – Species richness estimators curves of incidence (ICE)–, abundance (ACE)–coverage estimators, and CHAO2 for surveys of 2004 (**A**) and 2005 (**B**) in the Aberdare Mountain region and the Kajiado District (**C**). The first two letters refer to microhabitats types of aerial litter (AL), ground litter (GL), aerial bark (AB) and ground bark (GB). Note that some of the acronyms are hidden; however, species estimated can be obtained in Table one.

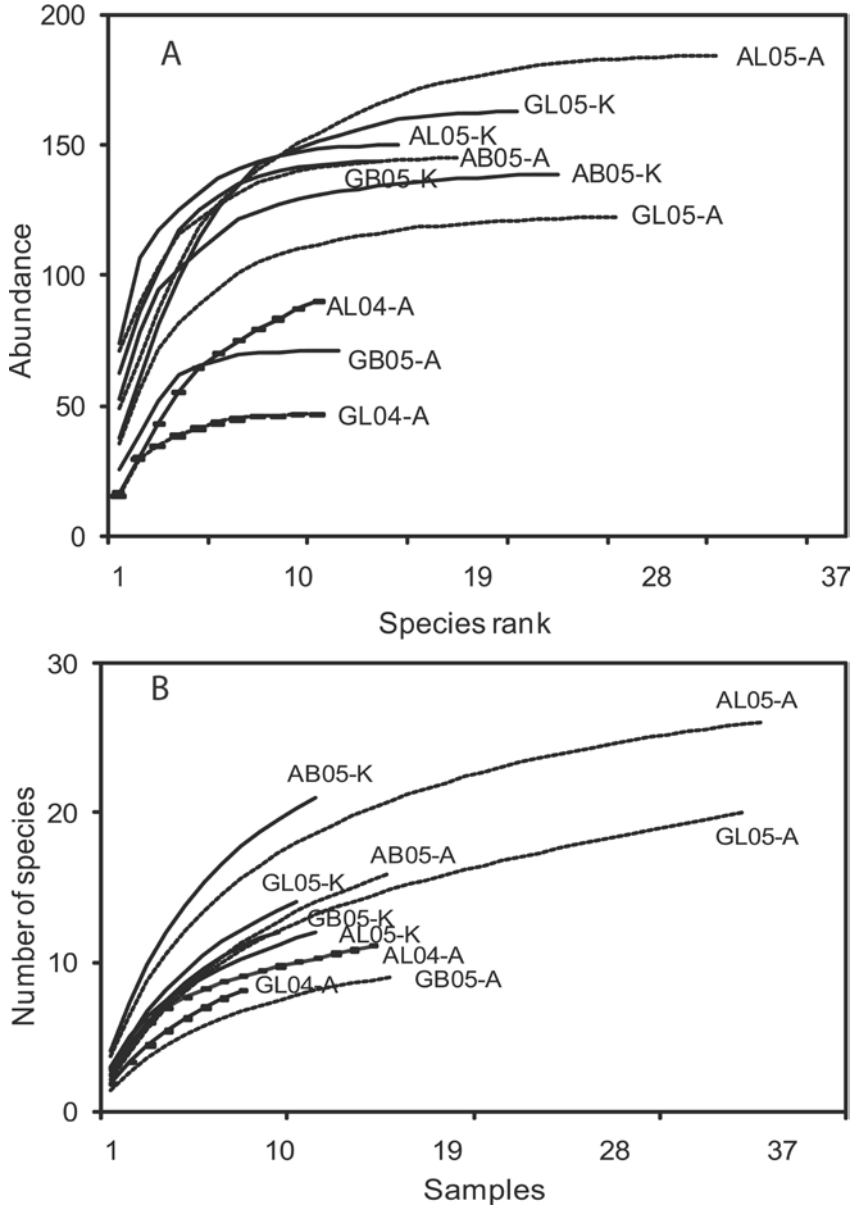

Fig. 3. – K–dominance (**A**) and sample–based rarefaction (**B**) curves. The first two letters refer to microhabitats (AL: aerial litter, GL: ground litter, AB: aerial bark, GB: ground bark), following two number are year of sampling (2004 or 2005) and last letter refer to Aberdare (A) or Kajiado (K) region.

Tab. 3. – Community similarity indices calculated using Morisita's index (upper right) and Horn's index of overlap (lower left).

	A–AL04	A–GL04	A–AL05	A–AB05	A–GL05	A–GB05	K–AL05	K–AB05	K–GL05	K–GB05
A–AL04	–	0.50	0.56	0.41	0.39	0.43	0.43	0.44	0.43	0.39
A–GL04	0.50	–	0.12	0.04	0.18	0.07	0.16	0.07	0.07	0.02
A–AL05	0.59	0.32	–	0.78	0.70	0.77	0.73	0.79	0.76	0.73
A–AB05	0.43	0.17	0.72	–	0.48	0.82	0.64	0.88	0.93	0.85
A–GL05	0.49	0.30	0.68	0.48	–	0.58	0.38	0.43	0.44	0.47
A–GB05	0.46	0.19	0.68	0.66	0.65	–	0.54	0.86	0.88	0.74
K–AL05	0.38	0.23	0.60	0.48	0.37	0.40	–	0.74	0.68	0.69
K–AB05	0.39	0.17	0.64	0.67	0.39	0.65	0.67	–	0.98	0.87
K–GL05	0.40	0.25	0.67	0.70	0.49	0.72	0.62	0.87	–	0.87
K–GB05	0.36	0.09	0.57	0.55	0.47	0.57	0.60	0.71	0.71	–

For the acronyms, the first letter signifies the two study areas in the Aberdare Mountain region (A) and the Kajiado District (K); the following two letters refere to microhabitats: aerial litter (AL), ground litter (GL), aerial bark (AB), ground bark (GB), and the numbers to the years of study: 2004 (04) and 2005 (05).

alpine, moderate for agricultural and arid lands and low for plantation, seasonal and montane forests. Among the different bark microhabitats, high species richness and abundances were recorded for arid and agricultural lands, moderate for subalpine/alpine on aerial bark and moderate on ground bark for arid lands. The numbers for common species were higher on litter than bark substrates in all land use types. Analyses of both ground and aerial litter microhabitats from the six land use/cover types using DCA to a certain degree gave unclear distribution patterns of both species and land use sites (Figure 5A and 5B). However, distinct communities were recognized for the alpine zones and arid lands on aerial litter and ground litter microhabitats, respectively. Species common on aerial litter in agricultural lands were *A. cinerea, D. effusum, P. depressa* and *Physarum melleum*; in seasonal forests *A. cinerea, D. difforme, P. depressa* and *P. didermoides*; montane forests *A. cinerea, D. effusum, D. difforme, P. depressa, P. compressum* and *P. didermoides*; subalpine/alpine *A. cinerea, D. effusum, D. subdictyospermum, D. anellus, D. difforme, D. saturnus, D. squamulosum, P. depressa, Physarum bivalve, P. cinereum, P. compressum* and *P. echinosporum*; and arid lands *A. cinerea, C. laxa, D. difforme, P. depressa, P. vermicularis, P. cinereum, P. compressum* and *P. pusillum*. Common species on ground litter consisted of *D. effusum, D. squamulosum, P. chrysosperma, P. depressa* and *S. fusca* var. *nigrescens* in agricultural lands, *D. effusum, D. difforme, D. iridis, D. squamulosum, P. chrysosperma, P. depressa* and *P. echinosporum* in montane forest; *Badhamia panicea, Collaria arcyrionema, D. effusum, D. subdictyospermum, D. difforme, D. squamulosum* and *P. echinosporum* in subalpine/alpine; and *P. depressa, P. cinereum, P. dider-*

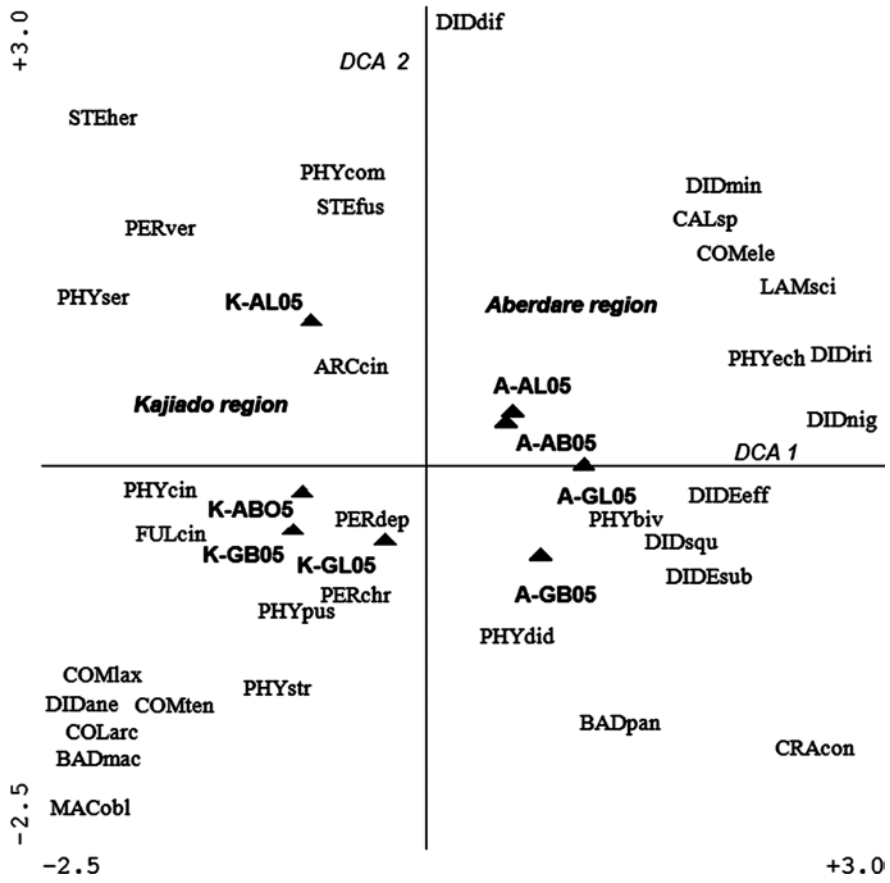

Fig. 4. – DCA biplot showing the distribution of common species in all microhabitats from both Aberdare and Kajiado regions. The variance explained by the first and second axes is 32% and 17% respectively. The full names for the abbreviated thirty three species used on the biplot is provided on Tables 2 and 5. The first letter on the microhabitat type refers to Aberdare (A) or Kajiado (K) region, next two letters refer to microhabitats: aerial litter(AL), ground litter (GL), aerial bark (AB), ground bark (GB) and the following two number are year of sampling (2004 or 2005).

moides, *P. pusillum* and *S. fusca* var. *nigrescens* in arid lands. *Perichaena chrysosperma* and *P. depressa* were the only species common on aerial- and ground bark microhabitats in agricultural lands, seasonal forests and dry lands.

Results of the ordinary least squares (OLS) fit of linear regression found no significant relationship existing between species richness and elevation or pH in most microhabitats. Significant relationships, how-

Tab. 4. – Comparison of species abundances and richness for the six land use/cover types. Mean values and standard deviation; number of samples or sites are given in parentheses.

	Land use/cover types[a]					
	Arid lands	**Agricultural lands**	**Plantation forest**	**Seasonal forest**	**Montane forest**	**Alpine/ subalpine**
Elevation (m)	600–2300	1830–2300	1785–2600	1915–2085	2230–3000	2970–3400
Mean species abundance (sporocarps per sample or 63.6 cm²)						
Aerial litter	120 ± 148 (15)	84 ± 134 (18)	66 ± 101 (6)	88 ± 117 (9)	194 ± 209 (15)	199 ± 142 (13)
Ground litter	119 ± 140 (15)	110 ± 184 (18)	16 ± 28 (6)	9 ± 13 (9)	57 ± 95 (15)	127 ± 150 (13)
Aerial bark	128 ± 172 (13)	212 ± 194 (12)	18 ± 25 (2)	60 ± 78 (5)	29 ± 26 (2)	113 ± 64 (2)
Ground bark	143 ± 89 (13)	44 ± 64 (12)	30 (1)	92 ± 103 (6)	10 ± 13 (3)	–
Species richness (mean species richness per sample/site[b])						
Aerial litter	15 (2.5 ± 1.8)	19 (2 ± 2.2)	11 (1.8 ± 1.8)	8 (2 ± 0.5)	24 (4.1 ± 2.1)	16 (3.5 ± 1.8)
Ground litter	21 (2.7 ± 2.6)	18 (2 ± 1.2)	3 (0.5 ± 0.8)	6 (0.8 ± 1.1)	3 (0.8 ± 0.9)	17 (2.6 ± 1.5)
Aerial bark	23 (3.9 ± 3.5)	12 (2.8 ± 2.3)	1 (0.5 ± 0.7)	4 (1 ± 0.7)	3 (1 ± 1)	5 (2.5 ± 0.7)
Ground bark	14 (2.4 ± 1.5)	7 (1 ± 0.9)	1	6 (1.3 ± 0.8)	3 (1 ± 1)	–

[a] Arid lands consisted of all study sites from the Kajiado District whereas the other five land use/cover were all found in the Aberdare Mountain region.
[b] Data used to calculate species abundances were the same as those used to determine species richness's means per site.

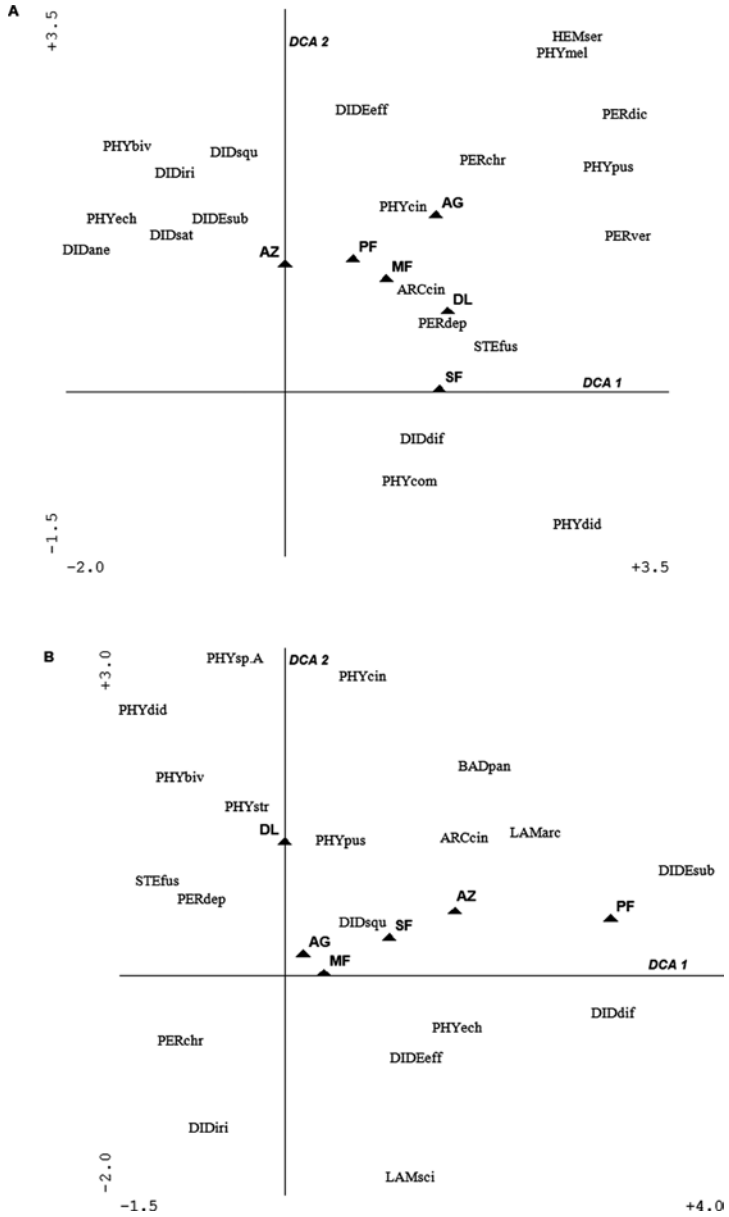

Fig. 5. – DCA biplots showing the distribution of common species from both Aberdare and Kajiado regions among the six land use/cover types on aerial litter microhabitats (A) and ground litter (B). The variance explained by the first and second axes is 41% and 6%, respectively for Fig. 5A and 31% and 19% for Fig. B. Twenty five species were used in each biplot and their full names are provided in Tables 2 and 5. Acronyms of samples refers to land use types of plantation forest (PF), seasonal forest (SF), montane forests (MF), alpine/sub alpine zone (AZ), agricultural (AG) and arid lands (DL).

ever, occurred between species abundances and elevation and pH on aerial litter in the Aberdare Mountain region ($r^2 = 0.38$, $F_{2,33} = 10$, $p = 0.0004$, with elevation having a strong effect, $p = 0.005$ and pH a mild impact $p = 0.07$) and ground bark microhabitats in the Kajiado District ($r^2 = 0.69$, $F_{2,7} = 7.7$, $p = 0.02$ with pH having a strong effect $p = 0.007$). These results were consistent with DCA analyses for aerial litter microhabitats where land use types and species were ordered along the elevation gradient.

Discussion

Sampling effort versus species richness

This study greatly increases our knowledge of myxomycetes in Kenya. The numbers of species obtained during this survey were comparable to those reported from other studies carried out elsewhere in the tropics in which similar methods were used (an overview of surveys and references is provided in Table 5). As already noted, the sampling carried out in the present study yielded an appreciable number of species (60) of which 51 were new records for Kenya, four were not previously reported in Africa. The few previously reported records in Kenya existed as field notes, citations in books, monographic reviews (Martin & Alexopoulos 1969, Eliasson & Lundqvist 1979), reports (Kost 2002) and databases on the internet (http://www.gbif.org/). Overall, a total of 70 species of myxomycete are now known from Kenya, which represents only a small percentage of all species known in Africa (24 % of 295, Ndiritu *et al*. 2009a) and in the world (8 % of 880 species, Hernández-Crespo & Lado 2005).

The performance of species richness estimators was in agreement with a number of findings that have found CHAO2 and ICE to be appropriate predictors of myxomycete richness (Unterseher *et al*. 2008). Unlike CHAO2 and ICE, ACE was found constantly to underestimate species richness which was in contrast to Chao *et al*. (2006) and Unterseher *et al*. (2008) who found them to be comparable. Chao *et al*. (2006) noted the performance of all the three nonparametric species richness estimators depends on sampling effort and underlying communities' species abundance distribution patterns. As it is evident in Figure 2, ACE seems to be very dependent on sample sizes that were inadequate or moderate on several microhabitats. Gatson (1996) observed that the major problem associated with species richness estimators is their dependence on sampling effort which unfortunately is rarely reported and thus impedes the comparison of the species richness from different localities or regions.

This initiative to survey most major microhabitats that myxomycetes are known to inhabit in several eco-climatic zones assisted in the documentation of a significant number of species. However, it is evident from the analyses that a significant number of species were missed

Tab. 5. – Occurrences and distribution of common myxomycetes in examples of tropical ecosystems as reported in the literature.

Ecosystem, elevation (m), localities and study period	Surveys (**FC**, **MC**). Microhabitats (GL, GW, GB, AL, AB). Total species recorded (**T**). Species occurrences: abundant (**A**), common (**C**). Percentage of sampling effort (**SE**) where known.
Neotropics	
[1] Lowland forests, Brazil, 400–950, 2 plots, 12 months	**FC**. **T**: 34. **A**: ARCcin, DIDcla, HEMcal, LAMsci, PHYalb, PHYpus. **C:** ARCden, CRIcan, DIDmin, LYCepi, PHYste, PHYvir, STEfus.
[2] Atlantic forest, Brazil, 2 y	**FC**. **T**: 33. **A**: ARCcin, TUBbom. **C**: ARCden, COLarc, CRIaur, CRImic, CRIten, HEMcal, HEMser, LYCexi, METves, PHYnuc, STEfus, STEaxi, TUBmic.
[3] Lowland Moist forest, Mexico, 500, 9 mo	**FC**. **T**: 33. **A**: ARCcin, HEMcal, HEMser, STEaxi. **C**: STEaxi, LYOepi, ARCden, STEtyp, METves, CRIten, STEfus.
[4] Tropical forests, Mexico, 15–1700, 14 d	**FC**, **MC**. **T**: 99. **A**: ARCcin, ARCden, CLAdeb, COMten, HEMcal, HERser, HERpad, PERchr, PHYste. **C**: CRIlan, CRImic, CRIvio, COLarc, DIDEspu, PERdep, STEaxi.
[5] Moist to wet forest, Puerto Rico, 350–1000, 1 mo.	**MC** (GL). **T**: 24. **A**: ARCcin, CRImic, STEfus. **C**: COMlax, DIDEeff, LAMsci, PHYalb, PHYmel.
[6] Moist, seasonal forest, Costa Rica, 10–1600, 10 plots, 7 y	**MC** (GL, AB). **T**: 60, **AB:** 25, **GL:** 43. **A**: ARCcin, COLarc, CRIvio, DIDiri, DIDsqu, LAMsci, MACsci, MACmar, PERver. **C**: ARCafr, DIDoch, DIDEhem, PERchr, PHYcom. **SE,** GL: 84; AB: 70.
[7] Moist forest, Costa Rica, 3100–3230, 3 plots, 7 mo	**FC, MC** (GL, GW, B). **T:** 37, **MC**: 4, **FC**: 34. **A**: CRIpir, CRImir, CRIvul, DIDsqu, HEMcal, HEMser (also abundant in **MC**), LAMcol, LYCepi, METflo, TRIbot, TRIfav, TRIver. **C**: CLAdeb, COMpul, CRIint, LAMech.
[8] Lowland moist forest, Cocos Island, Costa Rica, 5–576, 6 sites, 7 d	**FC**, **MC**. **T**: 41. **FC:** 4**, MC:** 37 (**AL**: 33, **GL**: 22, **B**: 10, **T**: 14)**. FC, A**: PHYmel. **MC, A**: ARCcin, COLarc, COMten, CRIten, CRImic, CRIvio, DIDEeff, PERchr, PERdep, STEfus. **C**: ARCmin, CLAdeb, COLlur, COMele, COMpul, DIAleu, DIDsqu, LAMsci. **SE,** AL: 62; GL: 69; B: 93; T: 88.
[9] Cloud forest, Ecuador, 1200–2720, 3 wk	**FC, MC** (GL, AL, AB, AE, AI, GW, AW)**. T**: 77 (**FC**: 67, **MC**: 27). **FC**, **A**: ARCcin, ARCden, CRAleu, DIDsqu, HEMcal, PHYcom, PHYpus; **C**: CRIcan, CRIten, DIDEeff, DIDEhem, DIDcla, DIDiri, DIDnig, HEMser, PHYdid. **MC**, **A:** ARCcin, DIDiri, DIDsqu, PHYcom; **C**: LAMsci, PERdic, PERver, PHYpus. **SE,** FC: 97; MC: 74–92.
[12]Neotropical world, 30 countries	**FC, MC**. **T**: 431. **A**: In this review 78 species found in ten or more countries were regarded as abundant or common. Myxomycetes not regarded as frequent in the above previous individuals surveys in Neotropical but were in this review arei: ARCinc, ARCins, ARCobv, COMnig, CRAten, CRIint, DIAbul, DICplu, DIDcla, DIDdif, DIDmel, ECHmin, FULsep, HEMcla, LICope, PHYobl, PHYbiv, PHYbog, PHYcin, PHYglo, PHYjav, PHYleu, PHYleuc, PHYten, RETjur, STElon, STEfla, STEher, STEpal, STEhyp, STEspl, STEtyp, TRIdec, TUBfer.

Tab. 5. – continued.

Ecosystem, elevation (m), localities and study period	Surveys (**FC**, **MC**). Microhabitats (GL, GW, GB, AL, AB). Total species recorded (**T**). Species occurrences: abundant (**A**), common (**C**). Percentage of sampling effort (**SE**) where known.
USA	
[17] Moist forests, Hawaiian Islands, 1982–90	**FC**, **MC**. **T**: 101. **A**: DIDEsau, HEMcal, PHYfla, PHYmel, PHYobl. **C**: ARCcin, COLarc, ECHmin, HEMser, PERchr, PERdep, STEaxi, STEfus, STEtyp, TRIfav.
Asia	
[18] Southern India, two localities, >1200, 1954–89.	**FC**, **MC** (GL, GW, GB). **T**: 99. **A**: ARCcin, DIDEeff, DIDcla, DIDsqu, LAMsci, PERdep, PHYcin, PHYech, PHYmel. **C**: ARCden, CRAleu, DIDEhem, DIDiri, DIDmin, DIDnig, FULsep, PERchr, PHYcom, PHYser.
[10] Forests, Thailand, 900, 5 plots, 12 mo.	**FC**. **T**: 62. **A**: ARCcin, CRAmin, DIDiri, DIDmin, DIDnig, LAMsci, PHYmel; **C**: ARCden, COLarc, DIDEhem, DIDcla, DIDsqu, HERser, LYCepi, PHYalb, PHYcin, PHYpus, PHYros, PHYvir, STEaxi, STEfus, STEnig.
[11] Forests, Thailand, 5 plots, 650–1700, 12 mo.	**FC**, **MC**. **T**: 70, **FC**: 53, **MC**: 33. **A**: ARCcin, ARCden, CRImic, DIDiri, DIDmin, DIDnig, LAMsci, PHYcin, PHYcom, PHYmel, PHYpus, PHYvir; **C**: COLarc, COMten, CRAmin, CRIaur, CRIcan, DIDEhem, DIDcla, DIDsqu, HEMser, LYCepi, PHYros, STEnig.
Africa	
[13] Tropical forests, Equatorial Guinea, 29 sites, 17 d.	**FC**. **T**: 40. **A**: ARCcin, ARCden, COLarc CRImic, CRIvio, HEMcal, HEMser, PHYste, STEfus, STEtyp. **C**: CLAdeb, CRIcan, LYCexi, METves, PERdep.
[14] Forests, Tanzania, 7 y	**FC**, **MC. T**: 105. **A**: ARCcin, ARCden, HEMcal. **C**: ECHmin, DIDsqu, FULsep, LICscy, PHYcom, PHYvir, STEfus.
[15] Forests and bushland, Kenya	**MC:** GL, GB, AL, AB. **T:** 60**. A:** ARCcin, PERchr, PERdep. **C**: COMele, COMlax, DIDEeff, DIDEsub, DIDane, DIDdif, DIDiri, DIDsqu, PERver, PHYcin, PHYcom, PHYdid, PHYech, PHYpus.
[16] African continent, 32 countries.	**FC**, **MC**. **T**: 295. **A**: ARCcin, ARCden, ARCinc, CRAleu, CRImic, CRIvio, DIAleu,, DIDEeff, DIDEhemi, DIDiri, DIDmel, DIDnig, DIDsqu, LYCepi, FULsep, HEMser, LAMsci, METves, PERcor, PERdep, PHYalb, PHYcin, PHYcom, PHYnuc, PHYpus, PHYvir, STEaxi, STEfus, STEspl, STEtyp.

Abbreviations used signify types of surveys: field collections (FC) and moisture chambers (MC). Microhabitats: ground litter (GL), ground bark (GB), aerial litter (AL), aerial bark of living trees (AB), bark (B), twigs (T), aerial epiphyte (AE), aerial inflorescences (AI), ground wood (GW), aerial wood (AW). Unless clarified after FC and MC, most species listed above were obtained from ground substrates. Full species names are ARCafr, *Arcyria afroalpina;* ARCcin, *A. cinerea*; ARCden, *A. denudata;* ARCinc, *A. incarnata;* ARCins, *A. insignis;* ARCmin, *A. minuta;* ARCobv, *A. obvelata;* CERfru, *Ceratiomyxa fruticulosa;* CERmor, *C. morchella;* CERsph, *C. sphaerosperma;* CLAdeb, *Clastoderma debaryanum;* COLarc, *Collaria arcyrionema,* COLlur, *C. lurida;* COMele, *Comatricha elegans;* COMlax, *C. laxa; COMnig, C. nigra;* COMpul, *C. pulchella;* COMten, *C. tenerrima;* CRAaur, *Craterium aureum;*

Tab. 5. – continued.

CRAleu, *C. leucocephalum;* CRAmin, *C. minutum;* CRIaur, *Cribraria aurantiaca;* CRIcan, *C. cancellata;* CRIint, *C. intricata;* CRIlan, *C. languescens;* CRImir, *C. mirabilis;* CRImic, *C. microcarpa;* CRIpir, *C. piriformis;* CRIten, *C. tenella;* CRIvio, *C. violacea;* CRIvul, *C. vulgaris;* DIAbul, *Diachea bulbillosa;* DIAleu, *D. leucopodia;* DICplu, *Dictydiaethalium plumbeum;* DIDEeff, *Diderma effusum;* DIDEhem, *D. hemisphaericum;* DIDEsau, *D. saundersii;* DIDEsub, *D. subdictyospermum;* DIDEspu, *D. spumarioides;* DIDane, *Didymium anellus;* DIDcla, *D. clavus;* DIDdif, *D. difforme;* DIDiri, *D. iridis;* DIDmel, *D. melanospermum,* DIDmin, *D. minus*; DIDnig, *D. nigripes,* DIDoch, *D. ochroideum;* DIDsqu, *D. squamulosum;* ECHmin, *Echinostelium minutum;* FULsep, *Fuligo septica;* HEMcal, *Hemitrichia calyculata;* HEMcla, *H. clavata;* HEMpar, *H. pardina;* HEMser, *H. serpula;* LAMcol, *Lamproderma columbinum;* LAMsci, *L. scintillans;* LAMech, *L. echinulatum;* LICper, *Licea operculata;* LICscy, *L. scyphoides*; LYCepi, *Lycogala epidendrum;* LYCexi, *L. exiguum;* MACmar, *Macbrideola martinii;* MACsci, *M. scintillans*; METflo, *Metatrichia floriformis*; METves, *M. vesparia;* PERchr, *Perichaena chrysosperma;* PERcor, *P. corticalis*; PERdic, *P. dictyonema;* PERdep, *P. depressa;* PERver, *P. vermicularis;* PHYobl, *Physarella oblonga*; PHYalb, *Physarum album;* PHYbiv, *P. bivalve;* PHYbog, *P. bogoriense;* PHYcin, *P. cinereum;* PHYcom, *P. compressum;* PHYdid, *P. didermoides;* PHYfla, *P. flavicomum,* PHYglo, *P. globuliferum;* PHYjav, *P. javanicum;* PHYleu, *P. leucophaeum;* PHYleuc, *P. leucopus;* PHYmel, *P. melleum;* PHYnuc, *P. nucleatum;* PHYpus, *P. pusillum;* PHYros, *P. roseum;* PHYste, *P. stellatum;* PHYten, *P. tenerum;* PHYvir, *P. viride*; RETjur, *Reticularia jurana*; STElon, *Stemonaria longa*; STEaxi, *Stemonitis axifera;* STEfus, *S. fusca;* STEfla, *S. flavogenita;* STEher, *S. herbatica;* STEnig, *S. nigrescens;* STEpal, *S. pallida;* STEspl, *S. splendens;* STEhyp, *Stemonitopsis hyperopta;* STEtyp, *S. typhina;* TRIbot, *Trichia botrytis;* TRIdec, *T. decipiens;* TRIfav, *T. favoginea;* TRIver, *T. verrucosa*; TUBbom, *Tubifera bombarda;* TUBfer, *T. ferruginosa;* TUBmic, *T. microsperma.*

Superscript number represent references: [1]Maimoni–Rodella and Gottsberger 1980, [2]Rufino and Cavalcanti 2007, [3]Ogata *et al.* 1996, [4]Lado *et al.* 2003, [5]Stephenson *et al.* 1999, [6]Schnittler and Stephenson, 2000, [7]Rojas and Stephenson 2007, [8]Rojas and Stephenson 2008, [9]Schnittler *et al.* 2002, [10]Tran *et al.* 2006, [11]Tran *et al.* 2008, [12]Lado and Wrigley de Basanta 2008, [13]Lado and Teyssiere 1998, [14]Ukkola 1998, [15]This study, [16]Ndiritu *et al.* 2009a, [17]Eliasson 1991, [18]Stephenson *et al.* 1993.

in the two regions surveyed. Some of the myxomycetes missed include (1) wood-inhabiting (lignicolous) myxomycetes that are difficult to culture using moist chambers cultures. Lignicolous species are normally collected in the field, a survey method not considered during this study, (2) species that may be associated strongly with some seasons, (3) dung-inhabiting (coprophilous) myxomycetes as a result of such substrates not being collected in our study, (4) small-sized myxomycetes (e.g., *Echinostelium* spp.) some of which are sometimes difficult to see using the moist chamber technique, and (5) inadequate sampling effort of microhabitats, such as those associated with bark substrates. Several ecological studies in the tropics where moderate to high numbers of species were recorded considered several seasons (Tran *et al.* 2006, 2008), a number of microhabitats (Schnittler and Stephenson 2000, Rojas and Stephenson 2008), had adequate sampling efforts (Schnittler *et al.* 2002) as well as surveys using both field and labora-

tory methods over a long period of time in a large survey area (Ukkola 1998). The detection of the small-sized corticolous myxomycetes can be studied easily using methods similar to those used to isolate protosteloid amoebae (Spiegel *et al.* 2007). These methods were successfully used to study the minute myxomycete, *Echinostelium bisporum* during surveys of protosteloid amoeba, which have apparently found this species to be common on several microhabitats in both tropics and temperate regions (Ndiritu *et al.* 2009b). The low number of corticolous species found inspite of the substantial number of bark cultures done was unusual; however, Schnittler *et al.* (2002) found similar results in cloud forest in Ecuador and attributed those results to prevailing wet conditions and constant environments below the tree canopy that do not favour myxomycetes growth and spores dispersal (Schnittler and Stephenson 2000).

Microhabitats' species abundance and distribution

Species diversities and abundances in the Aberdare Mountain region were found to be appreciably higher for aerial litter and aerial bark than for ground litter and ground bark microhabitats whereas those from arid sites were comparable among all microhabitats. Similar higher diversities for assemblages of myxomycetes associated with aerial microhabitats were also noted for tropical cloud forests in Ecuador (Stephenson *et al.* 2004) and tropical forests of Cocos Island in Costa Rica (Rojas & Stephenson 2008) as well as on tropical lianas of Cuba, Australia and Mexico (Wrigley de Basanta *et al.* 2008). Appreciable numbers of myxomycetes were also found on twigs and bark in the canopy of temperate forests (Schnittler *et al.* 2006, Stephenson *et al.* 2001, Snell & Keller 2003), whereas in the arid habitats of Big Bend National Park, USA, assemblages of myxomycete for both aerial and ground microhabitats were found to be rich and comparable (Ndiritu *et al.* 2009c). The consistent presence of significant numbers of myxomycetes on aerial microhabitats is interesting and has to a certain extent improved our knowledge on the distribution and occurrence of plasmodial slime molds. Nowadays, caution should be taken during interpretation of distribution patterns of earlier compiled myxomycetes data which were primarily obtained from ground substrates using either or both field collections and laboratory methods (e.g., Martin & Alexopoulus 1969, Alexopoulus 1970).

The reasons why myxomycetes are more abundant in aerial than ground microhabitats in wet tropical forests is not known. However, the fact that aerial and ground microhabitats in both arid and wet regions supported dissimilar species assemblages suggest that abiotic and biotic factors such as moisture gradients and vegetation cover which were strikingly different between the two regions' aerial and ground microhabitats were probably responsible for the observed pat-

tern. Unlike in arid areas, ground substrates in Aberdare forests were moist and permanently covered with understory plants (e.g., herbs and forbs). Aerial substrates in moist forests are open and easily available for spore to colonize while the fluctuating moisture conditions allow myxomycetes to establish, grow and disperse spores. Schnittler *et al*. (2002) noted that mesic forests are richer in myxomycetes because myxomycetes are best adapted to fluctuating moisture environments and are much less influenced by interspecific competition. Other reasons why myxomycetes are reduced on ground litter microhabitats perhaps include: (1) anoxic conditions due to high humidity and bacteria activities which create unfavourable micro-environmental conditions that inhibit growth of plasmodia, sporulation and/or the dispersal of spores, (2) competition with other microorganisms for food and space, (3) predation by other organisms such as insects and arachnids, and (4) presence of understory plants that increase cover to reduce air movement, accessibility and colonization of ground litter by spores (Stephenson *et al*. 1993).

Meanwhile the distribution, occurrence and abundance of some myxomycetes among the four major microhabitats were somehow comparable and species assemblages were slightly similar among related substrates of either bark or litter. This was an indication that substrate types determined the occurrence and abundance of myxomycetes. Although the moderate to high community similarity found among the four microhabitats was expected, our failure to classify further the four microhabitats (i.e. types of plants, substrates age) was perhaps responsible for the high similarity values obtained particularly of different substrates (microhabitats) from the same region. Stephenson (1988) noted that myxomycetes posses the attributes of r-selected strategists and can successfully exploit microhabitats that are both limited temporally and spatially. In addition, species with broad overall niche breadth are necessarily widespread and frequent while a significant percentage of species represented by narrow niche breadth are uncommon and rare. Stephenson *et al*. (2004) found wood-inhabiting myxomycetes to have high substratum specificity while litter, bark, inflorescences and epiphyllic liverworts had lower specificity values in cloud forests in Ecuador. In this study the three most abundant species (*Arcyria cinerea*, *Perichaena chrysosperma* and *P. depressa*) were widespread and inhabited all microhabitats though at different abundances. Correspondingly the other fifteen abundant or common species were found frequently in one or more but not all microhabitats whereas the 43 rare species were infrequent and random.

Relationship between myxomycetes and land use/cover

The associations between myxomycetes and land use/cover found were also evident in a number of ecological studies (Stephenson *et al*.

1999, Schnittler & Stephenson 2000, Tran *et al.* 2006, 2008). Generally land use/cover depends on elevation, temperature and moisture gradients that eventually determine plant diversity. All the six land cover types considered in this study supported significant numbers of species though species diversity varied between microhabitats. Study sites situated in the montane and alpine zones were characterized by high myxomycete diversity for both aerial litter and ground litter microhabitats. In similar habitats, significant numbers of myxomycetes were recorded in high elevation montane forests in Puerto Rico (Stephenson *et al.* 1999) and in Ecuador (Schnittler *et al.* 2002). Similarly, Tran *et al.* (2008) recorded substantial numbers of myxomycetes (44 species) in agricultural ground litter in Thailand during the period of one year. The few samples collected from arid lands showed that all microhabitats considered were productive and were comparable to other productive ecosystems such as tropical mesic and wet forests (Eliasson 1991). Unfortunately only a few ecological studies have been directed towards myxomycetes from arid ecosystems in the tropics (see Estrada-Torres *et al.* 2009). The few ecological surveys from temperate regions have found arid areas to be rich in myxomycetes, with different regions tending to support unique assemblages of myxomycetes (e.g., Kosheleva *et al.*, 2008, Ndiritu *et al.* 2009c). Meanwhile dryland vegetation (i.e. wood-, bush-, shrub lands) and tropical forests are consistently present throughout the African continent, and future surveys of these ecosystems might be very important in uncovering a rich myxomycete biodiversity of Africa that is still so poorly known to science.

Spatial and microhabitat differences in myxomycetes assemblages were evident and were attributed to several factors, most of which were not determined during this study. Elevation which can be interpreted as moisture-temperature complex gradient together with pH influenced myxomycetes in a manner observed in other studies. According to our analyses, only species found on ground bark in the Kajiado District and on aerial litter microhabitats in the Aberdare Mountain region had positive significant relationship with pH and elevation, respectively. Interestingly, whereas aerial microhabitats in Aberdare were species rich, ground bark from Kajiado were species poor. Maimoni-Rodella & Gottsberger (1980) and Ogata *et al. (*1996) found positive strong correlations between temperature, precipitation and myxomycete assemblages, whereas Rojas & Stephenson (2008) found similar trends between myxomycete diversity indices and both elevation and pH. Likewise, pH, water-holding capacity and decay stage of substrates were more important than variation in samples in explaining the occurrences of myxomycetes in Schnittler *et al.* (2006). In this study, the insignificant relationships found between species myxomycetes (e.g., richness and abundances) in some microhabitats were perhaps due to inadequate sampling effort occasioned by our rapid sampling regime which could have introduced noise and obstructed trends. Future stud-

ies should employ a more in depth sampling with a more robust experimental design (both in the field and laboratory) to understand how myxomycetes interacts with both abiotic and biotic factors.

Biogeography of myxomycetes in tropics

Early studies of myxomycetes in the tropics were geared towards taxonomy and species discovery with very little regard for their ecological requirements. However, since the 1980s, significant taxonomical and ecological work have assisted in the accumulation of information on myxomycetes from a number of countries in Central America, Asia and Africa (for references see Table 5; Lado & Wrigley de Basanta 2008 for a review of Neotropical myxomycetes). In most cases methods used to survey myxomycetes varied from one study to another depending on the survey objectives. However, information accumulated to date can be used to make some general statements with precautions concerning the occurrence and distribution of a number of myxomycete species reported in the tropics. To date, approximately 101 species from the tropics have been reported as abundant or common in one or more studies (Table 5). During this study 16 of those species were recorded as frequent (abundant or common) with another 22 species found occasionally or rarely in Kenya also reported as common or abundant in some other areas of the tropics (Tables 2 and 5). Interestingly, *D. subdictyospermum* and *D. anellus* were an exception as the present study was the first to report them as common anywhere in the tropics.

As mentioned above, more than half of the species recorded during this study are common or abundant throughout the tropics while the occasional or rare ones have also been encountered in other tropical areas. A closer look at frequent myxomycete species assemblages shows their abundances fluctuated from one area to another. This is an interesting ecological pattern and suggests that in, spite of myxomycetes being widespread, they can also have distinct biogeographic distribution patterns. In this study, *Arcyria cinerea* was the only species found abundantly in all studied areas in tropics and from the review in Table 5, one might be inclined to consider this species as ubiquitous and cosmopolitan. The other 15 species reported as frequent and widespread were either abundant or common in a few areas and occasional or rare in the other areas. For instance, *P. depressa* which was the most abundant species in this study was also abundant in Costa Rica and India, common in Hawaii, Mexico, West Africa and Central Africa and rare in Ecuador, Puerto Rico, Brazil and Thailand. Other frequent species in Kenya with similar disjunct distributional patterns include *C. laxa, D. effusum, D. difforme, D. squamulosum, D. iridis, D. saturnus, P. chrysosperma, P. vermicularis, P. cinereum, P. compressum, P. didermoides, P. echinosporum, P. pusillum* and *S. fusca* var. *nigrescens*.

The other species found frequently in other tropical regions displayed similar patterns (Table 5). It is obvious from these species' distributional patterns that the establishment and success of each particular species in each habitats had very little to do with availability of propagules but rather with other factors which were all beyond the scope of this study. The spatial dissimilarities in species abundances and composition may be attributed to many factors including dispersal mechanisms, varying environmental conditions at macrohabitats and microhabitats levels due to climate and substrates availability (e.g., Stephenson *et al*. 1993, Stephenson *et al*. 2000).

Comparison of species found in Kenya with those of high latitude zones (temperate and arctic) show some interesting similarities and dissimilarities especially for frequently recorded species. Just like in tropics, some of the abundant species in Kenya had a worldwide distribution, though for each species the occurrences and abundances varied from one region to another. In the meantime some general statements can be made on the global distribution of frequent myxomycetes recorded in Kenya. *Arcyria cinerea* which was one of the three most abundant species, has a worldwide distribution and almost all studies conducted to date have found this species in significant proportions in temperate regions (Stephenson 1989, Stephenson *et al*. 1993, Novozhilov *et al*. 2009, Everhart *et al*. 2008), the arctic (Stephenson *et al*. 2000) and the tropics (e.g., Lado & Wrigley de Basanta 2008, Ndiritu *et al*. 2009a). In this study *P. depressa* was the most abundant species, and its importance was also noted in some temperate forest in Germany (Schinttler *et al*. 2006), New Zealand (Stephenson 2003) and USA (Everhart *et al*. 2008). In addition notes from the aforementioned studies show that some of the species frequent in Kenya were also abundant in one or more higher latitudes areas, for example *C. laxa* (Iceland and Greenland in Arctic region, Colarado Plateau in USA, Volga River basin in Russia), *D. effusum* (temperate forests in USA), *D. anellus* (Kazakhstan, Mongolia, Volga River basin in Russia), *D. difforme* (Colarado Plateau in USA, Mongolia, Volga River basin in Russia), *D. iridis* (temperate forest in USA), *D. squamulosum* (New Zealand, Kazakhstan, Mongolia, Volga River basin, Siberia in Russia), *P. chrysosperma* (tundra in Northern Alaska, temperate forests in USA and Germany, Mongolia, Volga River basin in Russia), *P. vermicularis* (tundra in Northern Alaska, temperate forest in Germany, Kazakhstan, Mongolia, Volga River basin and Siberia in Russia), *P. pusillum* (New Zealand), *P. cinereum* (boreal forest in Russia, Volga River basin in Russia), *P. compressum* (New Zealand), *P. didermoides* (Mongolia), *P. straminipes* (Sonoran Desert in USA) and *S. fusca* (Arctic regions, temperate forest in Germany and USA). It is evident from these studies that most of all the locally abundant species have been recorded abundantly elsewhere in the world while a number of locally uncommon species have also been recorded as abundant in other areas.

Conclusions

In summary, the baseline data generated during this study improved our understanding of myxomycete abundance and distribution patterns in two regions of Kenya with contrasting ecological and climatic regimes. Unlike temperate regions, where myxomycetes are more abundant on ground substrates, myxomycetes were found to be more abundant on aerial substrates in these moist tropical habitats. The four microhabitats considered in arid regions were found to be important for myxomycetes, although ground litter and aerial bark seemed to be slightly richer than aerial litter and ground bark. Community structure was found to be more similar between samples of the same type of substrate material (e.g., ground litter-aerial litter, and ground bark–aerial bark microhabitats). Meanwhile, it is obvious from the species abundance distribution results (species estimators, diversity indices, rarefaction and rank classes) that a significant portion of the frequently occurring species were recovered but that most occasional and rare species were missed. Future studies should seek to document the latter in order to determine their commonness or rarity. Finally, more field and laboratory investigations should be carried out to determine how environmental factors interact with microhabitats and macrohabitats to influence myxomycete assemblages. Also poorly known is how propagule dispersal and intra- and interspecific species competition contribute to the observable species distribution patterns at local, regional, continental and global scale. Overall, there is still very little known about these aspects of the ecology of these organisms.

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