Soil-litter ant (Hymenoptera: Formicidae) community response to reforested lands of Gishwati tropical montane forest, northern-western part of Rwanda

Venuste Nsengimana[1,2] and Wouter Dekoninck[3]

[1]University of Rwanda, College of Education, School of Education, Department of Mathematics Science and Physical Education, Kayonza, Rwanda; [2]University of Rwanda, College of Science and Technology, Centre of Excellence in Biodiversity and Natural Resources Management, Huye, Rwanda and [3]Royal Belgian Institute of Natural Science (RBINS), 1000 Brussels, Belgium

Abstract

Recently, human activities have impacted biodiversity-rich forest in western Rwanda, creating a need to enhance restoration activities of degraded lands in the region. To evaluate the effects of reforestation activities on the community composition of soil-litter ants, research was conducted in Gishwati tropical montane forest, located in northern-western part of Rwanda. The ant fauna was studied in reforested lands dominated by regenerated native species and exotic tree species. Further, a primary forest made of native trees served as a reference. In each forest type, nine sampling points were used to sample ants. Ant specimens were collected using pitfalls, hand sampling and Winkler extractor. They were identified to subfamilies, genus and species levels using dichotomous keys, and also statistically analysed for species richness, diversity, evenness and community composition. We collected a total of 2,481 individuals from 5 subfamilies, 18 genera and 35 species. Higher abundance, diversity and species richness were found in soil-litter under natural primary and secondary forests dominated by regenerated native plant species compared to exotic tree forest. The ant community composition analysis indicated higher similarities in ant species sampled under primary native forest and secondary forest dominated by regenerated native species. Reforestation by regenerating native species may be given priority in restoration of degraded lands due to their importance in species richness and species diversity.

Introduction

Land use changes driven by anthropogenic activities are primary drivers of biodiversity loss and altering ecosystem function, especially in tropical biomes (Srivastava *et al.* 2019). A dominant human activity was clearing natural forests for development of agricultural activities (Czimczik *et al.* 2005). These activities are major drivers of habitat fragmentation (Alroy 2017) and forest cover loss globally (Yeshaneh 2015), currently reduced to 3% (Löf *et al.* 2019). Forest clearing is also a major driver of changes in vegetation structure (Karp *et al.* 2012), in light of shifts in forest dynamics (Chancellor *et al.* 2012a). Also, once a natural land is transformed into agricultural land, different management practices can affect flora and fauna of wild communities by reducing their food and giving place to predators (Bain *et al.* 2020). An example is the use of pesticides to protect crops from herbivory which may change species richness and diversity of invertebrates (Römbke *et al.* 2017). Another example is the use of chemical fertilizers to improve productivity, which may also cause changes in soil properties, and hence the community composition of soil fauna (Thorn *et al.* 2017; Yeshaneh 2015).

To improve and compensate land degradation ecologically, reforestation activities were applied in different countries (Kooch *et al.* 2018), by regenerating natural forests, or planting exotic tree species (D'Ippolito *et al.* 2013). Reforestation improves human livelihoods (Bullock *et al.* 2011), and provides goods such as firewood, timber and medicines to humans (Frolking *et al.* 2009). It provides also ecological services (Faber & Wensem 2012) such as water and air purification, erosion control and carbon harvesting (Vaglio *et al.* 2016). However, despite the advantages of reforestation, negative effects were also encountered in different areas, especially when non-native tree species are used (Quine & Humphrey 2010). Such reforestation decreases the vegetation cover of native species, consumes high soil nutrients and requires much water (Cao *et al.* 2009). Further, regeneration with non-native tree species can facilitate damaging invasions (Ren *et al.* 2009), and accelerate the loss of native species (Schlaepfer 2018).

To evaluate effects of land use change and reforestation activities on biodiversity, different studies have used invertebrates as biological indicators (Barlow *et al.* 2007; Solar *et al.* 2015)

through the assessment of their functions in an ecosystem (Ciaccia *et al.* 2019). In this perspective, soil-litter arthropod groups are a frequent focus (Maleque *et al.* 2009). The most common parameters assessed include changes in their occurrences, abundance and diversity (Yi & Moldenke 2005), as well as their ecological functions, such as the decomposition of organic matter (Magcale-Macandog *et al.* 2018). Among arthropods, ants (Hymenoptera: Formicidae) are preferred (Basset *et al.* 2015), based on the key functional roles ~~that~~ they play (Luke *et al.* 2014). These include maintaining soil health and soil fertility, recycling soil nutrients, energy flow, seed dispersal (del Toro *et al.* 2012) and soil turnover (Hill *et al.* 2008).

In addition, some ant species are successful colonizers of disturbed or restored habitats (Andersen & Majer 2004; Ferreira *et al.* 2016). Assessments of land use change therefore may focus on variation in ant species abundance, and overall ant community composition (Andersen & Majer 2004; Blinova & Dobrydina 2019; Tibcherani *et al.* 2018). However, few studies have assessed responses of ant species to forest disturbance (Leal & Filgueiras 2012; Vasconcelos & Bruna 2012; Vasconcelos *et al.* 2006), and no such study has been done in Rwanda. To fill this gap and provide a baseline data on effects of land use change on ant communities, the present study examined effects of land use change on ant communities in Gishwati forest, located in northern-western Rwanda.

Although some researchers studied the biodiversity of Gishwati (Chancellor *et al.* 2012a; Chancellor *et al.* 2012b; 2017; Inman & Ntoyinkama 2020; Kisioh 2015; Plumptre *et al.* 2007); less is known about its entomological diversity. Indeed, no research has been done on the diversity of ants in the area, and less is known about how reforestation activities affect the communities of ants. This study presents the first detailed study of ants in the area. It examined the response of soil-litter ant communities to reforestation in secondary forests composed of regenerated native and exotic tree species based on ants collected in 2019. We addressed three specific questions: (1) how do species richness and species composition of ants vary among natural and reforested lands? (2) how does species diversity vary in each studied forest type? and (3) what ant species are associated with each forest type? We hypothesized that natural and regenerated native forests would offer better conditions for ant species than the forest dominated by exotic plantations.

Materials and methods

Area of study

Gishwati forest is located in northern-western Rwanda (Figure 1), in the region of 1°36′52″, 1°52′17″ south, and 29°21′40″, 29° 28′50″ east. Its climate is that of the region, dominated by the rainfall. During the period of data collection, average rainfall was 1,823 mm during the rainy season (April–May) and 1,136 mm in the dry season (June–July). Temperature varied between 25°C and 26°C during the day, and between 13°C and 15°C during the night. Elevation varies between 2,020 and 2,500 m (Chancellor *et al.* 2012a), with the mean slope of 25.6°. This topography produces a wet valley in western part of the forest (Chancellor *et al.* 2012b). Gishwati forest is made of three fragments comprising the primary natural forest (Gishwati core), regenerated native tree species dominated by *Macaranga capensis* var *kilimandscharica*

and *Maesa lanceolata* located at Kinyenkanda, and reforested lands with *Acacia melanoxylon* and *Acacia mearnsii* tree species located at Nduruma (Figure 1).

The forest is part of the Albertine Rift, an area of conservation importance thanks to its richness in animal and plant biodiversity (Olson & Dinerstein 1998). The forest has been reduced gradually by human activities; its largest part being transformed into agricultural lands. It was reduced from its original 800,000 ha to 28,000 ha by the 1970s, and to 600 ha by 2005. Since then, restoration activities started, and 886 ha were designated as Gishwati core primary natural forest in 2007. In 2008, around 336 ha reforested with *Acacia* tree species were added to the core forest, and in 2009, other 262 ha of regenerated forest dominated by native trees, bamboo and fern species were incorporated in the forest. Gishwati is thus currently composed of 1,484 ha comprising natural land dominated by native primary forest, and reforested lands dominated by a secondary forest made of regenerated native species and exotic tree species (Courard-houri *et al.* 2016). Together with the neighbouring Mukura forest, Gishwati was decreed as Gishwati-Mukura National Park by the law N0 45/2015 on 15 October 2015 (GoR [Government of Rwanda] 2016).

The main purpose of creating the national park was the conservation of its biodiversity, much of it being endemic to the area. The forest is dominated by around 58 species of indigenous hardwood trees, bamboo and shrubs of particular conservation importance. Animal species identified in the forest include the eastern chimpanzee (*Pan troglodytes schweinfurthii*), the golden monkey (*Cercopithecus mitis kandti*) and the l'Hoest's monkey (*Cercopithecus l'hoesti*) (Chancellor *et al.* 2017). The forest is also home to other mammals such as red river hog (*Potamochoerus porcus*), black front duiker (*Cephalophus nigrifrons*), the southern tree hyrax (*Dendrohyrax arboreus*) and serval (*Felis serval*). Gishwati forest is also home to around 155 species of birds (Inman & Ntoyinkama 2020). Amphibians inhabiting the forest include the brown forest frog (*Litoria ewingii*) and different species of toads, while reptiles include the great lakes bush viper (*Atheris nitschei*) and different chameleon species (Kisioh 2015).

Sampling design and identification

In each forest type, nine sampling points of 1 m² quadrat were selected by leaving 5 m from the edge to avoid edge effects and keeping a distance varying between 300 and 400 m in the natural forest and between 500 and 600 m in the regenerated forest to avoid autocorrelation. At each sampling point, pitfall traps made of a water plastic bottle (6.5 cm diameter and 12 cm depth) were placed in a soil pit. Each trap was filled with a volume of 30 ml of 70% ethanol to capture and maintain captured ants. Traps were collected every 24 hours for two months in the rainy season (April–May) and two months in the dry season (June–July) in 2019. To collect a wide range of ants, data were also collected by hand sampling especially for foraging ants. Data were collected during 30 minutes at each sampling point, in a 1 m² quadrat (Tista & Fiedler 2011). Further, leaf-litter was collected at each sampling point and sieved through a Winkler extractor. Then, ant specimens were extracted from the litter using the dry sieve method (Wiezik *et al.* 2015). Each sampling technique was applied two times in each sampling points, and two times for each season, totalling 108 pitfall traps, 108 hand collections and 108 Winkler extractions.
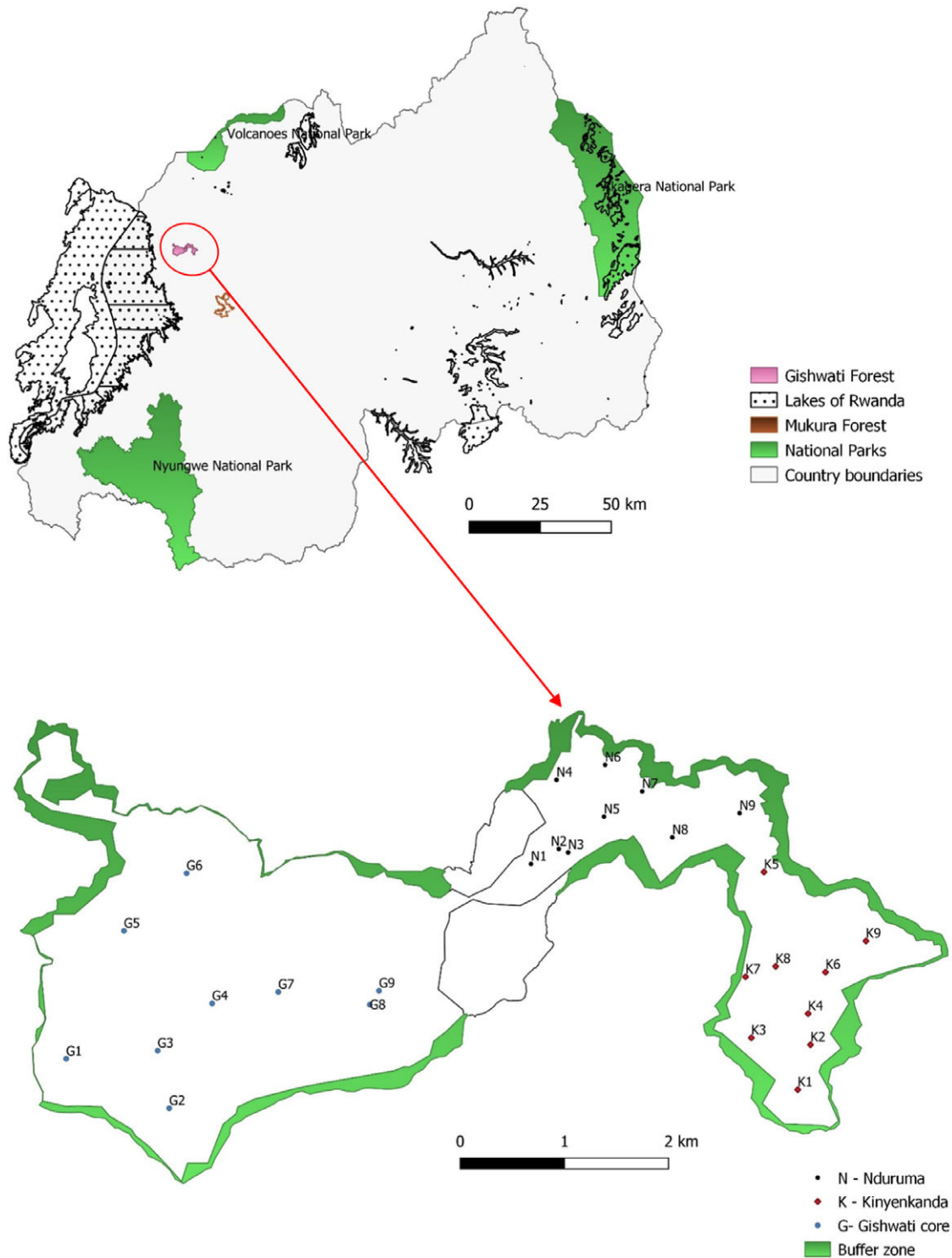
Figure 1. Location of Gishwati forest in Rwanda and location of sampling points in each forest type. G: Gishwati core primary forest, K: Kinyenkanda secondary forest (regenerated native tree species), N: Nduruma secondary forest (reforested with exotic tree species); numbers indicate sampling points pear each forest type.

Ants were first identified morphologically to subfamily and genus (Fisher & Bolton 2016). Next, specimens of each genus were identified to species via microscope and keys (Bolton & Fisher 2008; Borowiec 2016; Fischer *et al.* 2012; Rigato 2016; https://www.antsofafrica.org). When the name of the species was not found in the identification keys, the genus name was maintained, while the species name was designated by the abbreviation SP followed by the numbers from 01. For definitive confirmation of species names, samples were taken to the Royal Belgian Institute of Natural Science, Brussels, Belgium. There, each identified species was compared with image banks available on AntWeb database (AntWeb 2020), and ant collections of the museum. Specimens

are now housed at the Centre of Excellence for Biodiversity and Natural Resources Management (CoEB), College of Science and Technology, University of Rwanda.

Data analysis

Ant species richness was calculated based on total observed number of ant species per forest type, sampling technique and sampling points (Verdinelli *et al*. 2017). Diversity indices namely dominance (D′), Shannon (H′) and equitability (J′) were calculated for each forest type to provide more information on ant communities (Daly *et al*. 2018; Supriatna 2018). Further, the ANOVA tests were used for each forest to evaluate the variation in abundance of ant species between forest types (Etherington 2019; Itoh *et al*. 2010; Singhal & Rana 2015). Then, the abundance of ant species per sampling points and forest types were ordinated in non-metric multidimensional scaling (NMDS) based on Bray–Curtis similarity index (Taguchi & Oono 2005).

The Bray–Curtis similarity index was also used for analysis of similarity (ANOSIM) to test for the significant differences in species composition between sampling points and forest types (Clarke 1993). This was estimated following the R values. When R was closer to zero, we concluded a low dissimilarity (high similarity) between forest types. On the other hand, when R values were closer to 1, we concluded a high dissimilarity (low similarity) between forest types (Clarke & Green 1988). Finally, the similarity perecentage analysis (SIMPER) was calculated to determine which ant species contributed more to the similarity in species composition among forest types. High percentage implied high contribution, while low percentage explained low contribution to the similarity in species composition among forest types (Clarke 1993; Clarke & Green 1988). All calculations were performed using the Paleontological Statistics Software (PAST) version 4.02.

Results

We identified a total of 2,481 individuals belonging to 5 subfamilies, 18 genera and 35 ant species (Table 1). Higher ant abundance was found in native primary forest (43.1% of total abundance), compared to regenerated native species (32.3% of total abundance) and exotic tree species (24.6% of total abundance) of the secondary forests. Higher abundance of ants was collected by using pitfall traps (57.1% of the total abundance) compared to Winkler extractor (31.4% of the total abundance) and hand sorting (11.5% of the total abundance). Taking all results together, the subfamily Myrmicinae had higher total abundance (86.3%) than Formicinae (6.4%), Ponerinae (5.4%), Dorylinae (1.6%) and Pseudomyrmicinae (0.2%). The subfamily Ponerinae had more genera, while Myrmicinae had a higher number of species counted at 15. *Myrmicaria* SP03 had more abundance (46.6%) than other ant species (Table 1). The *Myrmicaria* SP03 differed from *Myrmicaria opaciventris* by the lack of ferruginous dull and in the structure of the postpetiole. It differed from *Myrmicaria congolensis* by the absence of densely packed fine longitudinal striations actually present at the dorsum of promesonotum in *Myrmicaria congolensis*. Further, *Myrmicaria* SP03 does not have the dull and red-brown gaster present in *Myrmicaria Congolensis*.

The total species richness was significantly higher in natural primary forest (mean = 30.5, Standard Error [SE] = 21.8), than the secondary forest with regenerated native (mean = 23.7, SE = 8.8, F = 0.1, $p > 0.05$), and exotic tree species (mean = 16.7, SE = 5.8, F = 0.4, $p > 0.05$). Different ant species were commonly found in primary natural forest (D′: mean = 0.5, SE = 0.1, $p < 0.05$), and in secondary forests of exotic tree species and regenerated native species (D′: mean = 0.2, SE = 0.0). However, the regenerated secondary forest had higher species diversity H′ (mean = 2.0, SE = 0.1), compared to secondary forest with exotic (mean = 1.9, SE = 0.1) and natural primary (mean = 1.1, SE = 0.1) forest. The species equitability (J′) in ant species identified in secondary forest with exotic trees was higher (mean = 0.8, SE = 0.1), than the equitability in the primary native forest (mean = 0.7, SE = 0.0), and the equitability in the secondary forest dominated by regenerated native species (mean = 0.5, SE = 0.0).

The NMDS based on Bray–Curtis similarity index between forest types indicated differences in sampling points (Stress = 0.14, $Axis_1$ = 0.71, $Axis_2$ = 0.15, $p < 0.05$, Figure 2). From Figure 2, it is also clear that the ant communities in Gishwati primary forest sampling points were different from that found in secondary forests. The ANOSIM by taking into consideration the whole community of ants indicated that species composition differed among forest types (R = 0.62. $p < 0.005$). High similarity in species composition was found between ant species collected under native primary forest and regenerated native secondary forest (R = 0.09, $p < 0.005$). Low similarity was found between ant species sampled under primary native tree forest and exotic secondary forest (R = 0.88, $p < 0.005$). This was also found in secondary forest, between the forests regenerated with native and exotic tree species (R = 0.75, $p < 0.005$).

The SIMPER showed that 13 ant species most contributed to the average dissimilarity among species assemblages (% dissimilarity > 1%). These are *Myrmicaria* SP03 (29.5, 38.5%: average dissimilarity and contribution), *Myrmicaria congolensis* (18.8, 24.5%), *Dorylus aggressor* (10.5, 13.7%), *Myrmicaria opaciventris* (3.3, 4.3%), *Tetramorium zonacaciae* (1.5, 2.0%), *Tetramorium simillimum* (1.12, 1.43%). *Tetramorium dedefra* (1.04, 1.36%), *Mesoponera subiridescens* (1.01, 1.31%) *Lepisiota* SP01 (1.0, 1.30%), *Tetramorium laevithorax* (0.98, 1.28%), *Camponotus maculatus* (0.94, 1.23%), *Camponotus flavomarginatus* (0.86, 1.13%) and *Tetramorium delagoense* (0.78, 1.01%). Other ant species showed little average dissimilarity and contribution percentage (% of dissimilarity less than 1%).

Discussion

High abundance of ant species was collected by using pitfall traps, and were found in soil-litter under natural primary forest compared to soil-litter under regenerated native and exotic tree species of the secondary forest. The ability of natural forests to maintain high soil biodiversity has been documented in other studies. It was found to be apparently based on elevated plant diversity and heterogeneity (Kassa *et al*. 2017), that offer nutrients to soil fauna (Bayranvand *et al*. 2017). It is also rooted on the forest canopy density that creates stable macroclimate environments (Kamau *et al*. 2017). The influence of environmental conditions and habitats created by primary forest on the abundance of ants was also confirmed by another study conducted in southern Cameroon (Borowiec 2016; Fotso *et al*. 2015).

Camponotus cinctellus and *Dorylus aggressor* were restricted to the primary native forest. Despite suitable conditions offered by the natural primary forest, these ant species might occur there due to their mode of life. The adaptations of the ants of the genus *Dorylus* might be influenced by their foraging habits and prey preferences. In this regard, most of *Dorylus* species are either subterranean, leaf litter or surface foragers (McIntyre *et al*. 2001; Vanthomme *et al*.

Table 1. Abundance of ant species per forest type (ns: number of specimens, NF: natural forest, EF: exotic forest, RF: regenerated forest, %: percentage)

| Subfamily and species	NF ns	NF %	EF ns	EF %	RF ns	RF %	Total ns	Total %
Subfamily: Dorylinae								
Dorylus agressor (Fabricus, 1973)	28	1.1					28	1.1
Dorylus congolensis (Santschi, 1910)	6	0.2			3	0.1	9	0.4
Dorylus fulvus (Westwood, 1839)	1	0.0			1	0.0	2	0.1
Subfamily: Formicinae								
Camponotus cinctellus (Gerstäcker, 1859)	6	0.2					6	0.2
Camponotus cognatocompressus (Forel, 1886)			18	0.7	6	0.2	24	1.0
Camponotus flavomarginatus (Mayr, 1862)			6	0.2	12	0.5	18	0.7
Camponotus maculatus (Fabricius, 1782)	6	0.2	20	0.8	21	0.8	47	1.9
Lepisiota SP01					18	0.7	18	0.7
Paratrechina longicornis (Santschi, 1920)			39	1.6			39	1.6
Polyrhachis gagates (Smith, 1858)			3	0.1			3	0.1
Polyrhachis militaris (Smith, 1858)			4	0.2			4	0.2
Subfamily: Myrmicinae								
Crematogaster nigriceps (Emery, 1897)					12	0.5	12	0.5
Meranoplus inermis (Emery, 1895)			15	0.6			15	0.6
Myrmicaria congolensis (Forel, 1909)	54	2.2	112	4.5	235	9.5	401	16.2
Myrmicaria opaciventris (Emery, 1893)	66	2.7	36	1.5	48	1.9	150	6.0
Myrmicaria SP03	766	30.9	174	7.0	216	8.7	1,156	46.6
Pheidole megacephala (Santschi, 1914)			12	0.5			12	0.5
Pheidole punctulata (Mayr, 1866)			6	0.2			6	0.2
Pheidole SP03			3	0.1			3	0.1
Pheidole SP04			3	0.1			3	0.1
Strumigenys sarissa (Bolton, 1983)	6	0.2			8	0.3	14	0.6
Tetramorium dedefra (Bolton, 1976)	20	0.8	24	1.0	30	1.2	74	3.0
Tetramorium delagoense (Forel, 1894)	18	0.7	13	0.5	43	1.7	74	3.0
Tetramorium laevithorax (Emery, 1895)	21	0.8	21	0.8	32	1.3	74	3.0
Tetramorium simillimum (Smith, 1851)	20	0.8	27	1.1	27	1.1	74	3.0
Tetramorium zonacaciae (Weber, 1943)	13	0.5	44	1.8	17	0.7	74	3.0
Subfamily: Ponerinae								
Bothroponera crassa (Emery, 1877)	2	0.1			3	0.1	5	0.2
Bothroponera kenyensis (Santschi, 1937)					6	0.2	6	0.2
Bothroponera talpa (André, 1890)	3	0.1			4	0.2	7	0.3
Hypoponera segnis (Bolton and Fisher, 2011)	5	0.2			7	0.3	12	0.5
Mesoponera subiridescens (Wheeler, 1922)	9	0.4	20	0.8	18	0.7	47	1.9
Odontomachus troglodytes (Santschi, 1914)	6	0.2			18	0.7	24	1.0
Megaponera analis (Fabricus 1793)	7	0.3	5	0.2	3	0.1	15	0.6
Phrynoponera gabonensis (André, 1892)	6	0.2	6	0.2	7	0.3	19	0.8
Subfamily: Pseudomyrmicinae								
Tetraponera natalensis (Forel, 1911)					6	0.2	6	0.2
Total number and % per forest type	**1,069**	**43.1**	**611**	**24.7**	**801**	**32.3**	**2,481**	**100**
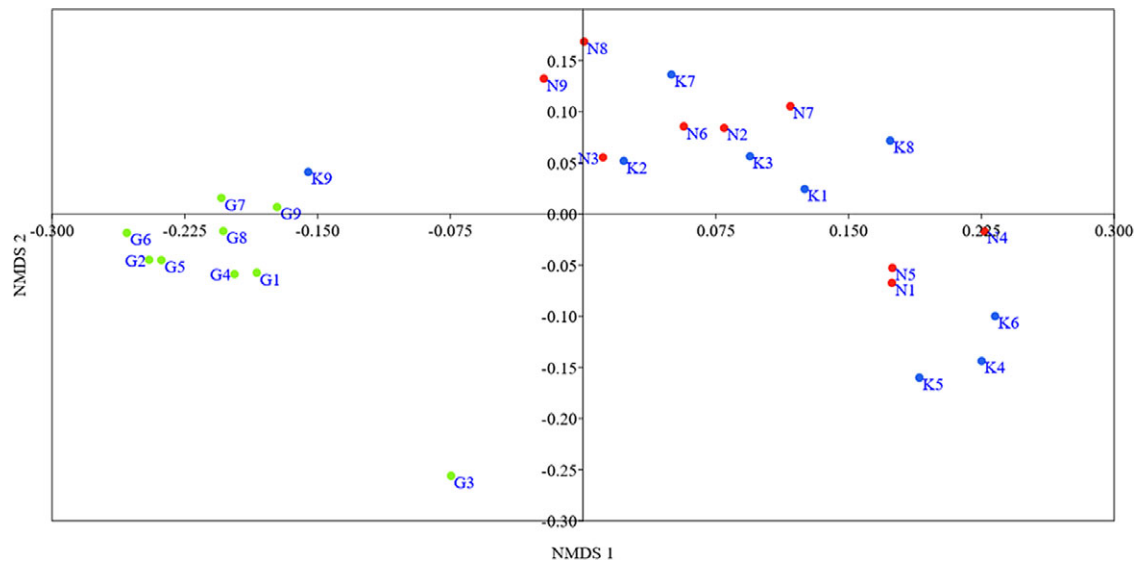
Figure 2. Non-metric multidimensional scaling (NMDS) based on the Bray–Curtis similarity index between the forest types (G: Gishwati core natural primary forest, N: Nduruma land (dominated by exotic tree species), K: Kinyenkanda land (dominated by regenerated native species). The numbers correspond to the sampling points.

2017) so that they may occur in all land types. Another study indicated that the *Camponotus cinctellus* is able to survive in most environmental conditions (Nsengimana *et al.* 2018) mainly in open landscapes such as savannah and cleared forests (Pekár & Haddad 2011), and tolerates different land uses (Quine & Humphrey 2010). The occurrence of *Camponotus cinctellus* in natural forest might be associated with the effects of human activities that cleared the forest mainly for agricultural activities.

Eight species of the genera *Meranoplus*, *Polyrachis*, *Pheidole* and *Paratrechina* were restricted to the exotic forest. Our results also indicated that exotic tree species had less abundance of ant species, cases observed also in another study which indicated that exotic tree species have little relevance for biodiversity conservation (Martin *et al.* 2012). They induce the extinction of native species by favouring opportunistic invasive species (Rundel *et al.* 2014). Another study indicated that non-native forest plantations affect soil water resources, and change soil physical, chemical and biological characteristics (Boudinot & Fisher 2013; Chomicki & Renner 2017).

Back to the genus *Meranoplus*, available information about the mode of life of the genus is limited. Most species nest directly in the soil, under stones, in rotten wood or in leaf litter (Anderson 2006). However, further studies may focus on the mode of life of the species *Meranoplus inermis* as available information is more generalized to the genus level. In relation to the genus *Polyrachis*, the species *Polyrhachis militaris* is an arboreal ant species. Another study indicated that the species has the ability of changing habitats from arboreal to subterranean (Robson & Kohout 2007). However, nothing is known if this is the same case for the species *Polyrhachis gagates*. Occurrence of these species in exotic forest type might be due to their adaptations to the environmental conditions imposed by open and disturbed exotic forest type (Underwood & Brian 2006).

Exotic forest was also dominated by the highly invasive *Pheidole megacephala*. Another study indicated that this species is adapted to different land uses mainly cleared, open (Vanderwoude *et al.* 2000) and disturbed environments (Kouakou *et al.* 2017). Another study showed that *Pheidole megacephala* is a highly invasive species (Horwood 1988), able to gradually replace native ants

(AntWeb 2020). The forest is also inhabited by *Pheidole punctulata*, which, like *Pheidole megacephala*, has the ability to survive in different types of habitats. It was commonly found in open woodlands, human settlements, tropical dry forest and along the roads (AntWeb 2020). Its specific microhabitat preferences include dead trees, spaces under rocks and tree barks, living and dead tree branches (Kouakou *et al.* 2017). The occurrence of *Pheidole punctulata* and *Pheidole megacephala* and their restriction to the secondary forest made of exotic tree species might be related to their adaptations to the conditions and structure of the secondary forest.

Exotic tree species were also dominated by the species *Paratrechina longicornis*, which is also an invasive species with the ability to survive in disturbed environments. This species is mainly found in urban centers, gardens and other manmade structures in cool temperate climates (Bini *et al.* 2013). Its occurrence in exotic tree species might be associated with the adaptations to the conditions imposed by the disturbed and open secondary forest dominated by exotic tree species.

Five ant species were restricted to the regenerated secondary forest made of native trees: *Bothroponera kenyensis*, *Lepisiota* SP01, *Tetraponera natalensis* and *Crematogaster nigriceps*. Little information is known about the mode of life of ants from the genus *Bothroponera* (Hita & Fischer 2014; Hita *et al.* 2010a, 2010b). Concerning the genus *Lepisiota*, a recent study indicated that all ants from the genus are generalist foragers with diverse nesting habitats, including decaying woods, soil and living trees (Sharaf *et al.* 2016). Even though they were restricted to regenerated native species in this study, *Lepisiota* species actually have the ability to occur in different types of wild habitats (Chazdon *et al.* 2009). In relation to the species *Tetraponera natalensis*, another study indicated that the survival of the species is more linked to its competitive character (Blüthgen & Stork 2007). Where they occur, they eliminate many other insects and remain the only dominant species in the area (Palmer & Brody 2007). This mode of life probably allows them to adapt and survive the conditions imposed by the regenerated native species habitats.

Besides *Tetraponera natalensis*, survival of the species *Crematogaster nigriceps* was found to be related to their ability to fight other herbivores and being aggressive to browser insects

(Stanton *et al.* 1999). They mainly depend on the axillary and terminal shoots of the host trees as source of food (Fernandes *et al.* 2014). Their presence in regenerated forest might be associated with the availability of young axillary and terminal shoots of young tree species.

Two ant species occurred in both native and exotic secondary forests. These are *Camponotus flavomarginatus* and *Camponotus cognatocompressus*. Recent studies indicated that these species prefer soft wood and young trees that offer suitable areas for nest construction (Chomicki & Renner 2017; Kamau *et al.* 2017; Sayad *et al.* 2012). The occurrence of these species might be associated with young trees found in the studied secondary forests which are still young with soft woods.

Further, seven species were found in both primary native forest and secondary forest dominated by regenerated native tree species: *Bothroponera crassa*, *Bothroponera talpa*, *Dorylus congolensis*, *Dorylus fulvus*, *Hypoponera segnis*, *Odontomachus troglodytes* and *Strumigenys sarissa*. The occurrence of these different ant species in primary native and secondary regenerated native forest types may depend on either suitable environmental condition offered by native tree species, even though the mode of life of each ant species has also to be considered (Kronauer *et al.* 2007). *Odontomachus troglodytes* for instance is a very common and wide-spread wood ant species in Central Africa (Booher 2019) as well as *Botrhoponera talpa* (Joma & Mackay 2015). Little information about the mode of life is available for *Dorylus congolensis* (Bolton & Fisher 2011), *Hypoponera segnis* (Raimundo *et al.* 2009) and *Strumigenys sarisa* (del Toro *et al.* 2012).

Twelve ant species occurred in all forest types (Table 1). As it was discussed in the previous paragraphs, less is known about the mode of life of *Camponotus* species. This is the same for the species under the genus *Mesoponera*. However, the occurrence of ant species under the genus *Myrmicaria* in all forest types can be associated with their mode of life as it was found in other studies. The species *Myrmicaria congolensis* and *Myrmicaria opaciventris* are predators (Andersen & Majer 2004), tropical climate specialist (Hernández-Ruiz *et al.* 2009) and generalized Myrmicinae (Kenne & Dejean 1999), that have the ability to adapt to all environmental conditions (Kenne & Dejean 1999). The occurrence of these species as well as *Myrmicaria* SP03 in all forest types might be related to their adaptations to different environmental conditions imposed by forest types (Yusuf *et al.* 2013).

Another species found in all studied forest types is *Megaponera analis*. During the field data collection, we have mainly found this species in soil-litter rich in termites. The association between *Megaponera analis* and termites was found to be related to the ~~their~~ mode of feeding habits of the ant species, which mainly rely on termites as a major source of food (Hita *et al.* 2010). Further, all species under the genus *Tetramorium* identified in this study occurred in all studied forest types (Table 1). The little-known information about the mode of life of the ant species under *Tetramorium* genus indicated that they are predominant in old world, few of them being introduced in the new world (Hita & Fischer 2014). They are mainly found in Afrotropical region, where they inhabit a wide range of microhabitats. This mode of life indicates the diversification of *Tetramorium* species in Afrotropical region (Hita & Fischer 2014).

Conclusion

Results of this study indicated high ant species richness and species diversity in a primary forest and regenerated secondary forest using native tree species. This indicates the role of native primary forests and restoration activities using native tree species to maintain and pursued high biological diversity. We conclude that primary and secondary forests dominated by native species play a more significant role in ant biodiversity conservation compared to the secondary forest dominated by exotic tree species. We recommend further studies to focus on more ant collections and to the mode of life of each identified ant species and to understand the adaptations of each ant species to a specific forest type.

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