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Widespread Distribution of Highly Adapted *Bradyrhizobium* Species Nodulating Diverse Legumes in Africa

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Bradyrhizobium is one of the most cosmopolitan and diverse bacterial group nodulating a variety of host legumes in Africa, however, the diversity and distribution of bradyrhizobial symbionts nodulating indigenous African legumes are not well understood, though needed for increased food legume production. In this review, we have shown that many African food legumes are nodulated by bradyrhizobia, with greater diversity in Southern Africa compared to other parts of Africa. From a few studies done in Africa, the known bradyrhizobia (i.e., *Bradyrhizobium elkanii, B. yuanmingense*) along with many novel *Bradyrhizobium* species are the most dominant in African soils. This could be attributed to the unique edapho-climatic conditions of the contrasting environments in the continent. More studies are needed to identify the many novel bradyrhizobia resident in African soils in order to better understand the biogeography of bradyrhizobia and their potential for inoculant production.

Keywords: biogeography, cowpea, groundnut, Bambara groundnut, wild legumes, soil factors, novel species

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INTRODUCTION

Globally, farmers depend on N fertilizers for increased crop yields (Crews and Peoples, 2004). Even then, sub-Saharan Africa currently uses the least chemical fertilizers compared to other regions (Ruben et al., 2007), due largely to high cost of these inputs for resource-poor farmers, their inaccessibility and potential to pollute the environment, as well as poor infrastructure (Dakora and Keya, 1997; Chianu et al., 2011). These factors together have limited the use of N fertilizers in African agriculture, even though there is a growing demand for increased crop production to feed the growing population (Dakora and Keya, 1997; Aticho et al., 2011; Chianu et al., 2011; Lal and Stewart, 2013). To feed the expected 2.5 billion people by 2050, Africa will need to roughly double its agricultural production. Food production is, however, associated with environmental pollution from anthropogenic activity. For example, the current level of industrialization has been achieved with 70% of the water used by people, 80% of deforestation worldwide, 70% loss of biodiversity and nearly one-quarter of the total greenhouse gas emissions (Tilman et al., 2011; Kessy et al., 2016). The world therefore urgently needs to increase agricultural productivity in a sustainable and environmentally-friendly manner. The large increase in population observed today would require at least 20% increase in crop yields in order to meet global food/nutritional security (Evans and von Caemmerer, 2011). This in turn may require the expansion of agricultural activity into marginal and/or non-arable land in order to feed the growing human population (Hungria and Vargas, 2000).

Africa is one of the major centers of legume diversity in the world, and is therefore home to a large number of indigenous legume species (Sprent, 2009; Beukes et al., 2013). In Africa, grain legumes remain the key source of dietary protein and starch (Bezner Kerr et al., 2007). Legumes also serve as high protein feed for livestock production, and biofertilizer for maintaining soil productivity. Therefore, legume inclusion in cropping systems has the potential to increase crop yields, which are currently very low at farm level in Africa when compared to the rest of the world (Akibode, 2011). Furthermore, N_2 fixation in legumes can provide economic, environmental and agronomic benefits to farmers in Africa where socio-economic conditions are poor (Chianu et al., 2011; Siddique et al., 2011). It is thus not surprising that BNF is the most important biological process on earth after photosynthesis (Unkovich et al., 2008) as it not only reduces fossil energy use globally, but also sustainably promotes increased agricultural yields without environmental damage. BNF is, however, influenced by many factors, which include geographic location, soil type, host–plant genotypes, and the rhizobial symbionts (Jaiswal et al., 2017).

Of the proteobacteria, *Bradyrhizobium* is an ancestral symbionts and highly cosmopolitan in terms of its distribution as a free-living bacterium in different habitats and in symbiosis with diverse leguminous hosts (Sprent et al., 2017). Like other N_2-fixing microsymbionts, *Bradyrhizobium* exhibits a bipartite life cycle which alternates between the free-living state in soils and as a symbiotic partner inside root nodules of legumes. Its chromosome is also bipartite in nature, with the main chromosomal genes being largely expressed under free-living conditions, and symbiosis genes expressed *in planta*. The plasmids or genomic island of root-nodule bacteria harbor all the symbiotic genes, which are usually transmitted vertically, or horizontally between different chromosomal backgrounds.

The interaction of legumes with root-nodule bacteria has become a model for dissecting the molecular conversation between rhizobial strains and their host plants, and is the best understood mutualistic relationship, especially when compared to other systems such as the mycorrhizal symbiosis with land plants and the Frankia symbiosis with actinorhizal plants.

While we currently have a clearer understanding of the molecular signals involved in the early stages of nodule formation, these insights get masked by the diversity of legumes and their rhizobia, as well as the ecological niches that interact to produce root nodules. As a result, we do not know how natural selection shapes each partner, as well as the extent to which the interaction can vary depending on intrinsic and extrinsic factors.

Also, we still do not understand the community structure and composition of bradyrhizobia found in African soils, even though we know that only certain types of bradyrhizobia are known to nodulate the diverse range of legumes grown in Africa (see **Figure 1**). Studies based on a few African countries seem to suggest that the number, species and strains of bradyrhizobial populations found in African soils are individually and collectively much greater than that shown in **Figure 1**. Only future studies will unravel the scale of novel bradyrhizobia resident in African soils that are waiting to be discovered and identified using modern molecular technologies. This review summarizes the status of legume root nodulation by bradyrhizobia in Africa.

LEGUMES NODULATED BY *Bradyrhizobium* SPECIES IN AFRICAN SOILS

Reports on legume nodulation by *Bradyrhizobium* in Africa are rather scanty in terms of (i) the diversity of legumes studied (ii) the types and numbers of bradyrhizobial microsymbionts found to nodulate legumes in Africa, and (iii) the huge number of unknown bradyrhizobial isolates waiting to be delineated and identified. In our laboratory alone, we have studied and reported on the nodulation of cowpea (*Vigna unguiculata* L. Walp), Bambara groundnut (*Vigna subterranean* L. Verdc), Kersting's bean (*Macrotyloma geocarpum* Harns), groundnut (*Arachis hypogaea* L.), common bean (*Phaseolus vulgaris* L.) and soybean (*Glycine max* L. Merr) in different agro-ecologies of selected African countries, which include Ghana, South Africa, Ethiopia, Mozambique, Zambia, Swaziland, and Mali. This review is a summary of our work together with those of others reported from across Africa. In this study, we intend to summarize data on *Bradyrhizobium* nodulation of cowpea, groundnut, soybean and Bambara groundnut together with data on nodulation of other wild African legumes by bradyrhizobia.

DIVERSITY OF MICROSYMBIONTS NODULATING INDIGENOUS *Vigna* SPECIES IN AFRICA

Cowpea (*Vigna unguiculata* L. Walp.) is a major food crop in Africa, its organs such as leaves, green pods and grain are eaten as a source of protein (Pule-Meulenberg et al., 2010). It is a promiscuous legume that is often used to trap microsymbionts in soil during diversity studies (Guimarães et al., 2012; Costa et al., 2013; Jaramillo et al., 2013; Grönemeyer et al., 2015a, 2016; Chidebe et al., 2018). This legume can establish effective symbioses with diverse bacterial species belonging to the genera *Rhizobium* and *Bradyrhizobium* (Wade et al., 2014; Chidebe et al., 2018). As a result, cowpea has the ability to grow in diverse environments where other legumes may fail to survive. The cowpea symbiosis can meet up to 96% of the plant's N requirement, and contribute substantially to the N needs of subsequent cereal crops, especially where the soils are nutrient-poor (Peoples et al., 2009; Belane and Dakora, 2010). Some studies have shown that cowpea can derive as much as 66% or more of its N nutrition from symbiotic fixation in Botswana (Pule-Meulenberg and Dakora, 2009), up to 99% in Ghana (Naab et al., 2009), and 15–56% in Zimbabwe (Ncube et al., 2007). These differences in N obtained from symbiosis can be attributed to the functional diversity among the *Bradyrhizobium* strains nodulating cowpea in Africa (Pule-Meulenberg et al., 2010; Grönemeyer et al., 2014; Chidebe et al., 2018).

Earlier studies have identified *Bradyrhizobium* as the dominant microsymbiont nodulating cowpea in Botswana,

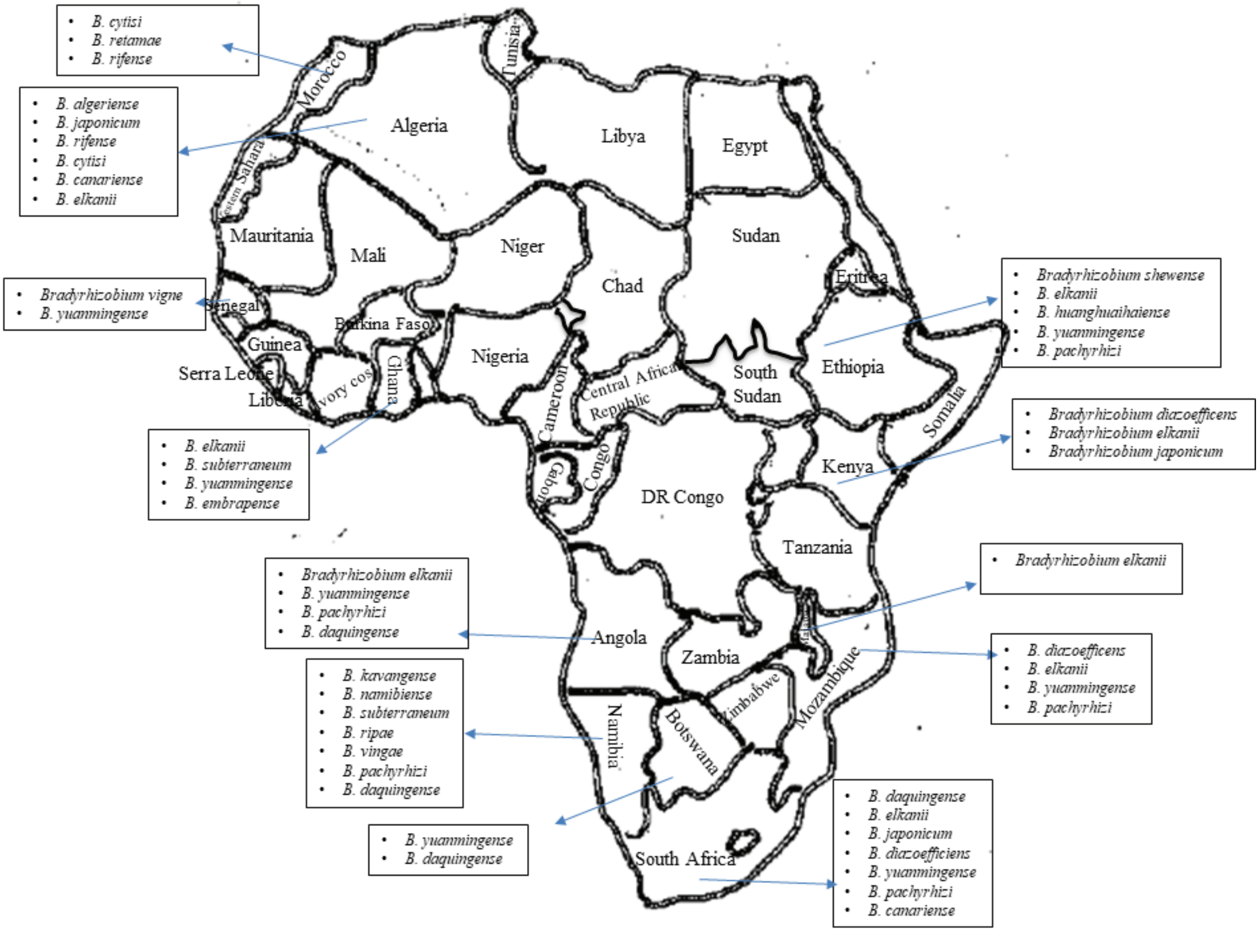

FIGURE 1 | Presence of diverse bradyrhizobial population in African soils.

Ghana, South Africa (Steenkamp et al., 2008; Pule-Meulenberg et al., 2010); Senegal (Wade et al., 2014), Mozambique (Chidebe et al., 2018), Ethiopia (Degefu et al., 2017), and Angola, as well as Namibia (Grönemeyer et al., 2014). Cowpea microsymbionts have a broad host nodulation range (Mpepereki et al., 1996). However, Africa is vast and agro-ecologically divergent, therefore many more studies are needed on the diversity and phylogeny of cowpea-nodulating microsymbionts in the continent, the center of its origin and diversification. The characterization of native rhizobia from the different geographic regions of Africa is likely to increase our understanding of their contribution to ecosystem functioning and thus help to unravel the factors shaping microsymbiont diversity and distribution in African soils.

Perhaps because Africa is the origin of cowpea, there is a vast diversity of cowpea rhizobia present in African soils (Steenkamp et al., 2008; Pule-Meulenberg et al., 2010; Wade et al., 2014; Degefu et al., 2017; Chidebe et al., 2018). This would be consistent with the view that the sites of origin of legumes tend to coincide with the centers of diversity of their associated microsymbionts needed for nodule formation and N_2 fixation (Puozaa et al., 2017). Furthermore, it has been argued that because Brazil and the Southern African region share similar climatic conditions (Chibeba et al., 2017) is probably the reason why only Southern Africa and Brazil have added more novel *Bradyrhizobium* species to that genus nodulating cowpea. The first cowpea-nodulating *Bradyrhizobium* was identified in the Amazon soils of Brazil, and classified as *Bradyrhizobium manausense* (Silva et al., 2014). Later, two *Bradyrhizobium* species [i.e., *Bradyrhizobium kavangense* (Grönemeyer et al., 2015b) and *B. vignae* (Grönemeyer et al., 2016)] were isolated from cowpea root nodules in Southern Africa (Namibia and Angola, respectively). More recently, *B. brasilense* (da Costa et al., 2017) was also identified in Brazilian soils (**Table 1**).

In a similar study, the soils of Botswana exhibited considerable diversity in the *Bradyrhizobium* species, (namely, *B. yuanmingense, B. daquingense* and a novel *Bradyrhizobium* sp.) that nodulated cowpea (Steenkamp et al., 2008). Studies in Senegal (West Africa) also revealed novel *Bradyrhizobium* species as the bacterial symbionts of cowpea, and these were closely related to *B. yuanmingense* (based on six loci sequence analysis) but symbiotically grouped with *B. arachidis* based on *nodC* and *nifH* gene analysis (Wade et al., 2014). A taxonomic

TABLE 1 | Morph-physiological and general characteristics of *Bradyrhizobium* type strains.

Species name	Legume host	Origin	Tolerance to NaCl	Temperature range for growth (°C)	pH	Growth rate (h) and colony size (mm)	Reference
B. americanum	*Centrosema macrocarpum*	Venezuela	<1%	15–35	6–8	–(<1)	Ramírez-Bahena et al., 2016
B. arachidis	*Arachis hypogaea*	China	< 1%	20–30	6–8	8.8(–)	Wang R. et al., 2013
B. algerians	*Retama sphaerocarpa*	Algeria	1%	28–30	4–8	14–23(–)	Ahnia et al., 2018
B. betae	*Beta vulgaris*	Spain		28–30	7.5		Rivas et al., 2004
B. brasilense	*Vigna unguiculata*	Brazil			4–10		da Costa et al., 2017
B. cajani	*Cajanus cajan*	Dominican Republic		18–37	5–9		Araújo et al., 2017
B. canariense	*Chamaecytisus proliferus*	Spain		28–30	4–7		Vinuesa et al., 2005
B. centrolobii	*Centrolobium paraense*	Brazil	<1%	20–36	5–11	–(3–4)	Michel et al., 2017
B. centrosemae	*Centrosema molle*	Venezuela	1%	10–37	4.5–7.5	–(<1)	Ramírez-Bahena et al., 2016
B. cytisi	*Cytisus villosus*	Morocco	<0.25	14–30	6–8		Chahboune et al., 2011
B. daqingense	*Glycine max*	China	1%	28–37	6–9	10 (1)	Wang J.Y. et al., 2013
B. denitrificans	–	Germany		28–41			Van Berkum et al., 2006
B. diazoefficiens	*Glycine max*	Japan	<1%	28	4.8–6.8	–(1.2–1.5)	Delamuta et al., 2013
B. elkanii	*Glycine max*	United States					Kuykendall et al., 1992
B. embrapense	*Desmodium heterocarpon*	Brazil	<1%	28–37	4.5–8.0	7.49(–)	Delamuta et al., 2015
B. erythrophlei	*Erythrophleum fordii*	China	1%	4–60	5–8	14.6 (<1)	Yao et al., 2015
B. ferriligni	*Erythrophleum fordii*	China	1%	4–45	5-8	13.1 (1)	Yao et al., 2015
B. forestalis	Amazon legume tree	Brazil	<1%	15–37	4–10	–(>1)	da Costa et al., 2018
B. ganzhouense	*Acacia melanoxylon*	China	3%	4–37	5–12	–(1–2)	Lu et al., 2014
B. guangdongense	*Arachis hypogaea*	China	1%	15–28	5–7	16.94 (1–2–)	Li et al., 2015
B. guangxiense	*Arachis hypogaea*	China	1%	15–28	5–7	13.49(1–2)	Li et al., 2015
B. huanghuaihaense	*Glycine max*	China	<1%	10–37	6–9	7–9 (1)	Zhang et al., 2012
B. icense	*Phaseolus lunatus*	Peru	1%	28	5.5–10	11–12(1)	Durán et al., 2014a
B. ingae	*Inga laurina*	Brazil, Roraima	<0.5%	15–32	4–8	9.5(1)	da Silva et al., 2014
B. iriomotense	*Entada koshunensis*	Japan, Okinawa	<1%	15–32	4.5–9.0		Islam et al., 2008
B. japonicum	*Glycine max*	Japan	<2%	25–30	3.5–9.0	–(<1)	Jordan, 1982
B. jicamae	*Pachyrhizus erosus*	Honduras	1%	5–32	6–8	–	Ramírez-Bahena et al., 2009
B. kavangense	*Vigna unguiculata*	Namibia, Kavango	<1%	28–38	5–9	7.5 (0.2–0.8)	Grönemeyer et al., 2015b
B. lablabi	*Lablab purpureus*	China	<1%	10–37	5–10	10–12(<1)	Chang et al., 2011
B. liaoningense	*Glycine max*	China	<1%	25–30	7.45–8.08	–(0.2–1)	Xu et al., 1995
B. lupini	*Lupinus angustifolius*	United States	<1%	28	7		Peix et al., 2015
B. manausense	*Vigna unguiculata*	Brazil	<0.05	15–32	4–8	7.8 (1)	Silva et al., 2014
B. macuxiense	*Centrolobium paraense*	Brazil	<1%	20–36	5–11	–(3–4)	Michel et al., 2017
B. mercantei	*Deguelia costata*	Brazil	<1%	28–30	4.5–8	–(<1)	Helene et al., 2017

(Continued)

TABLE 1 | Continued

Species name	Legume host	Origin	Tolerance to NaCl	Temperature range for growth (°C)	pH	Growth rate (h) and colony size (mm)	Reference
B. namibiense	*Lablab purpureus*	Namibia		–			Grönemeyer et al., 2017
B. neotropicale	*Centrolobium paraense*	Brazil, Roraima	<1.5%	15–37	4–10	10.8 (1)	Zilli et al., 2014
B. oligotrophicum	Rice	–	<0.5	28–37	–	–	Ramírez-Bahena et al., 2013
B. ottawaense	*Glycine max*	Canada	<1%	20	5–10	12–13(<1)	Yu et al., 2014
B. pachyrhizi	*Pachyrhizus erosus*	Honduras	<1%	5–37	4.5–8	–	Ramírez-Bahena et al., 2009
B. paxllaeri	*Phaseolus lunatus*	Peru	1%	28–37	5.5–10	11–12(1)	Durán et al., 2014a
B. retamae	*Retama sphaerocarpa*	Morocco	<1%	14–30	6–8	–(<1)	Guerrouj et al., 2013
B. rifense	*Cytisus villosus*	Morocco	<1%	14–30	4.5–8.0	(<1)	Chahboune et al., 2012
B. ripae	*Indigofera rautanenii*	Namibia					Bünger et al., 2018
B. sacchari	*Sugar cane*	Brazil	<0.5	20–37	5–12	–(1.5–2)	de Matos et al., 2017
B. shewense	*Erythrina brucei*	Ethiopia	0.5%	15–30	5–10	–(1–2)	Aserse et al., 2017
B. stylosanthis	*Stylosanthes guianensis*	Brazil	<1%	28	4.5–8.0	(1–1.34)	Delamuta et al., 2016
B. subterraneum	*Vigna subterranea*	Namibia, Kavango	<1%	28–37	5–9	8 (0.2−1)	Grönemeyer et al., 2015a
B. tropiciagri	*Neonotonia wightii*	Brazil	<1%	28	4.5–8.0	7.42(–)	Delamuta et al., 2015
B. valentinum	*Lupinus mariae-josephae*	Spain	<1%	14–30	4–10	–(<2)	Durán et al., 2014b
B. vignae	*Vigna unguiculata*	Namibia	<1%	28–40	5–9	8 (0.2–1)	Grönemeyer et al., 2016
B. viridifuturi	*Centrosema pubescens*	Brazil	<1%	28	4.5–7.0	(0.5–1.5)	Helene et al., 2015
B. yuanmingene	*Lespedeza cuneata*	China	<1%	25–30	6.5–7.5	9.5–16(<1)	Yao et al., 2002

revision of these novel *Bradyrhizobium* species showed that they belonged to *B. vignae*, which was originally isolated from cowpea nodules collected from Namibia (**Figures 2**, **3**).

In studies of cowpea in the Okavango of Namibia, *B. pachyrhizi* was found to dominate in the acidic soils, while cowpea nodulation in the semi-humid region of Angola and Namibia was by diverse bradyrhizobial strains, most of them relating to *B. yuanmingense* and *B. daqingense,* as well as by some novel *Bradyrhizobium* species (Grönemeyer et al., 2014), which were later identified as *B. kavangense,* and *B. vignae* (Grönemeyer et al., 2015b, 2016).

Chidebe et al. (2018) recently found high molecular diversity among 122 microsymbionts isolated from Mozambican soils and characterized using BOX-PCR analysis, a finding confirmed by multilocus sequence analysis which showed that cowpea is nodulated by different *Bradyrhizobium* species (*B. elkanii, B. yuanmingense, B. diazoefficiens, B. pachyrhizi*, and novel *Bradyrhizobium* species), as well as by diverse *Rhizobium* species (*Neorhizobium galegae, Rhizobium pusense,* and *Rhizobium tropici*).

The Guinea savanna and Sudano-Sahelian regions of Ghana, as well as the low veld of South Africa were also explored for the biogeographic distribution of root-nodule bacteria nodulating cowpea in the two countries. In that study, sequence analysis of core genes (*atpD*, *glnII*, *gyrB*, and *rpoB*) and symbiotic genes (*nifH* and *nodC*) revealed the presence of highly diverse *Bradyrhizobium* species nodulating cowpea that were closely related to *B. daqingense, B. subterraneum, B. yuanmingense, B. embrapense, B. pachyrhizi,* and *B. elkanii,* as well as a number of unidentified novel *Bradyrhizobium* isolates (Mohammed et al., 2018). Multivariate analysis also showed that the distribution of these *Bradyrhizobium* species was strongly influenced by the concentration of mineral nutrients in the soils (Mohammed et al., 2018).

Some of the previously reported novel *Bradyrhizobium* sp. from Ghana, Senegal, Angola, Namibia, South Africa, and Mozambique, as well as those from our study were reanalyzed phylogenetically using previously and newly listed *Bradyrhizobium* type strains in the GenBank. The results showed that only the Senegalese isolates initially considered to be novel,

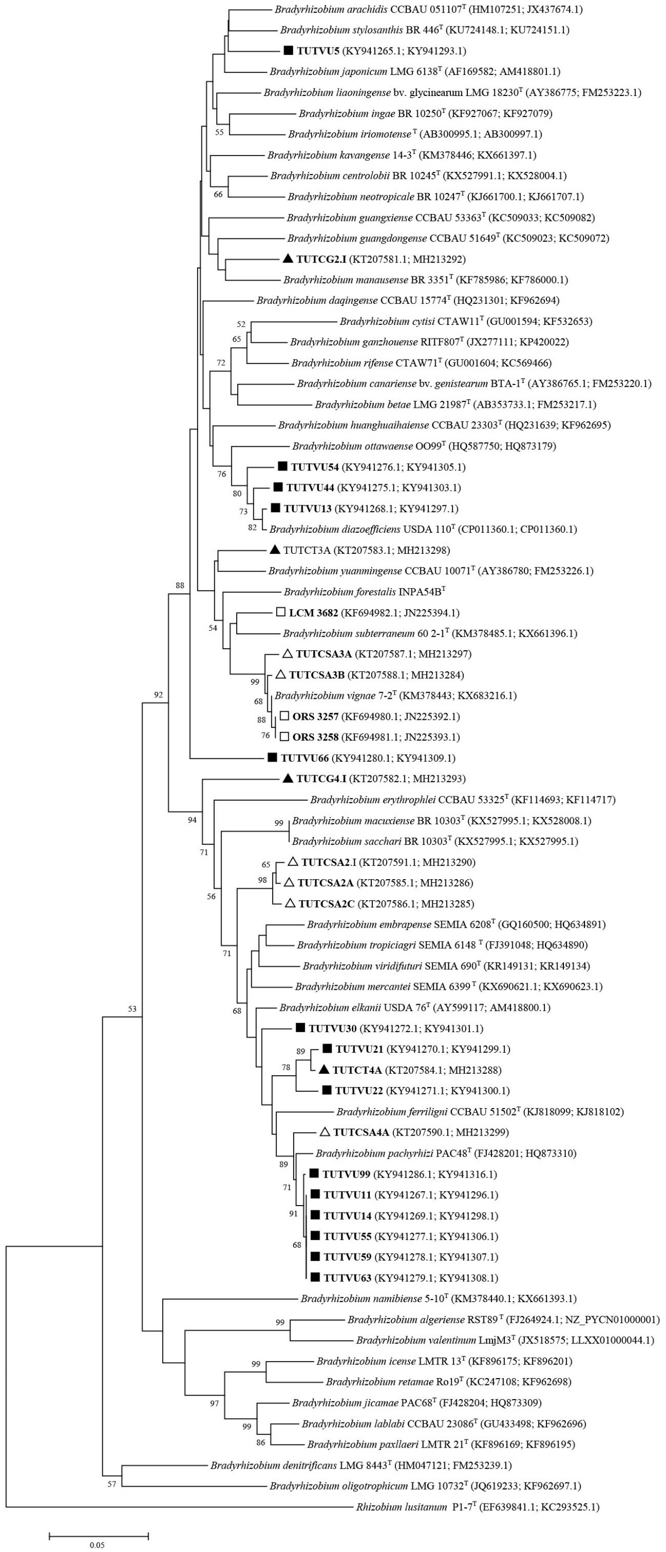

FIGURE 2 | Neighbor-joining molecular phylogenetic analysis of cowpea nodulating rhizobia from ▲Ghana, □ Senegal, ■ Mozambique, and △ South Africa based on concatenated *glnII* + *gyrB* (495 bp) sequences with type strains of *Bradyrhizobium* species. The evolutionary history was inferred by using the Neighbor-joining method based on the Kimura 2-parameter model. The scale bar indicates the number of substitutions per site. The percentage of trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. All positions containing gaps and missing data were eliminated. Evolutionary analyses were conducted in MEGA6.

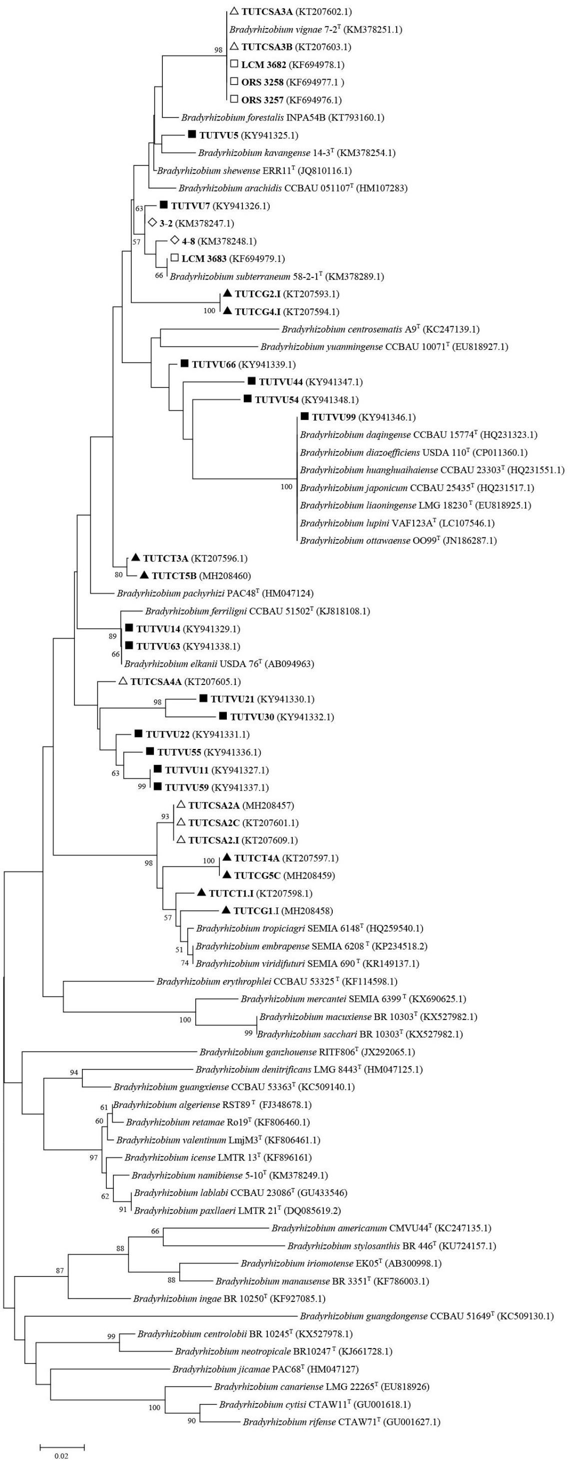

FIGURE 3 | Neighbor-joining molecular phylogenetic analysis of cowpea nodulating rhizobia from ▲Ghana, ☐ Senegal, ■ Mozambique,◇ Namibia△ and South Africa based on *nifH* (401 bp) sequences with type strains of Bradyrhizobium species. The evolutionary history was inferred by using the Neighbor-joining method based on the Kimura 2-parameter model. The scale bar indicates the number of substitutions per site. The percentage of trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. Evolutionary analyses were conducted in MEGA6.

were actually strains of *B. vignae*, while all the others remained novel *Bradyrhizobium* sp. with no alignment to any reference type strains in the GenBank (see **Figures 2–4**).

After cowpea, Bambara groundnut (*Vigna subterranea* L. Verdc.) is the second most important indigenous non-commercial food legume in Africa both in consumption and land area under cultivation. It is cultivated across the entire African continent, from Mauritania and Senegal in the West to Uganda and Tanzania in the East, and from Mali and Sudan in the North to South Africa, Zimbabwe, and Swaziland in the South. Bambara groundnut is cultivated as a sole or mixed culture (Doku, 1995), and is drought-tolerant, as well as performs well in very nutrient-poor soils due to its ability to form effective symbiosis with soil rhizobia that reduce atmospheric N_2 to ammonia (Puozaa et al., 2017). Nitrogen contribution by Bambara groundnut under field and glasshouse conditions can vary significantly, with values ranging from 4 to 200 kg N ha^{-1} (Gueye and Bordeleau, 1988; Kumaga et al., 1994; Kishinevsky et al., 1996; Nyemba and Dakora, 2010; Mohale et al., 2013).

Analysis of nodules from Angola and Namibia have suggested that Bambara groundnut is nodulated by a diverse group of *Bradyrhizobium* species (Grönemeyer et al., 2014). Using RFLP analysis of root-nodule bacteria collected from South Africa, as well as the Guinea and sahelian Savanna of Ghana, Puozaa et al. (2017) found that diverse bradyrhizobia nodulate Bambara groundnut in those regions. These indigenous bradyrhizobia were closely related to *B. vignae* (Puozaa et al., 2017), which nodulates *Vigna subterranea*, *Vigna unguiculata*, *Arachis hypogaea,* and *Lablab purpureus* (Grönemeyer et al., 2014). However, some novel monophyletic groups were also identified which suggested the presence of novel *Bradyrhizobium* in the soils studied. Caballero-Mellado and Martinez-Romero (1996) have argued that the origins of legumes tend to coincide with the centers of diversity of their specific symbiotic bacteria. This supports the large diversity of *Bradyrhizobium* species found to nodulate Bambara groundnut in Africa (Grönemeyer et al., 2014; Puozaa et al., 2017), the center of origin of this legume. Taken together, the reports of various studies appear to suggest that *Vigna* species in Africa are largely nodulated by *Bradyrhizobium* bacteria. The huge functional diversity among microsymbionts nodulating *Vigna* indicate the potential for exploiting these diverse rhizobial populations for use as inoculants to increase cowpea and Bambara groundnut production in Africa.

SOYBEAN NODULATION BY *Bradyrhizobium* SPECIES

Soybean (*Glycine max* L. Merr.) belongs to the tribe *Phaseoleae,* sub-tribe *Glycininae,* and genus *Glycine*. It originated from north-eastern China and is presently cultivated worldwide under various climatic conditions (Appunu et al., 2008; Risal et al., 2010; Singh, 2010). Soybean was probably introduced into Africa by Chinese traders traveling along the east coast of Africa in the 1800s (Shurtleff and Aoyagi, 2009). The average soybean yield in Africa is 1.0 ton per hectare compared with the world average of 2.35 ton per hectare (Abate et al., 2012). Africa is one of the largest

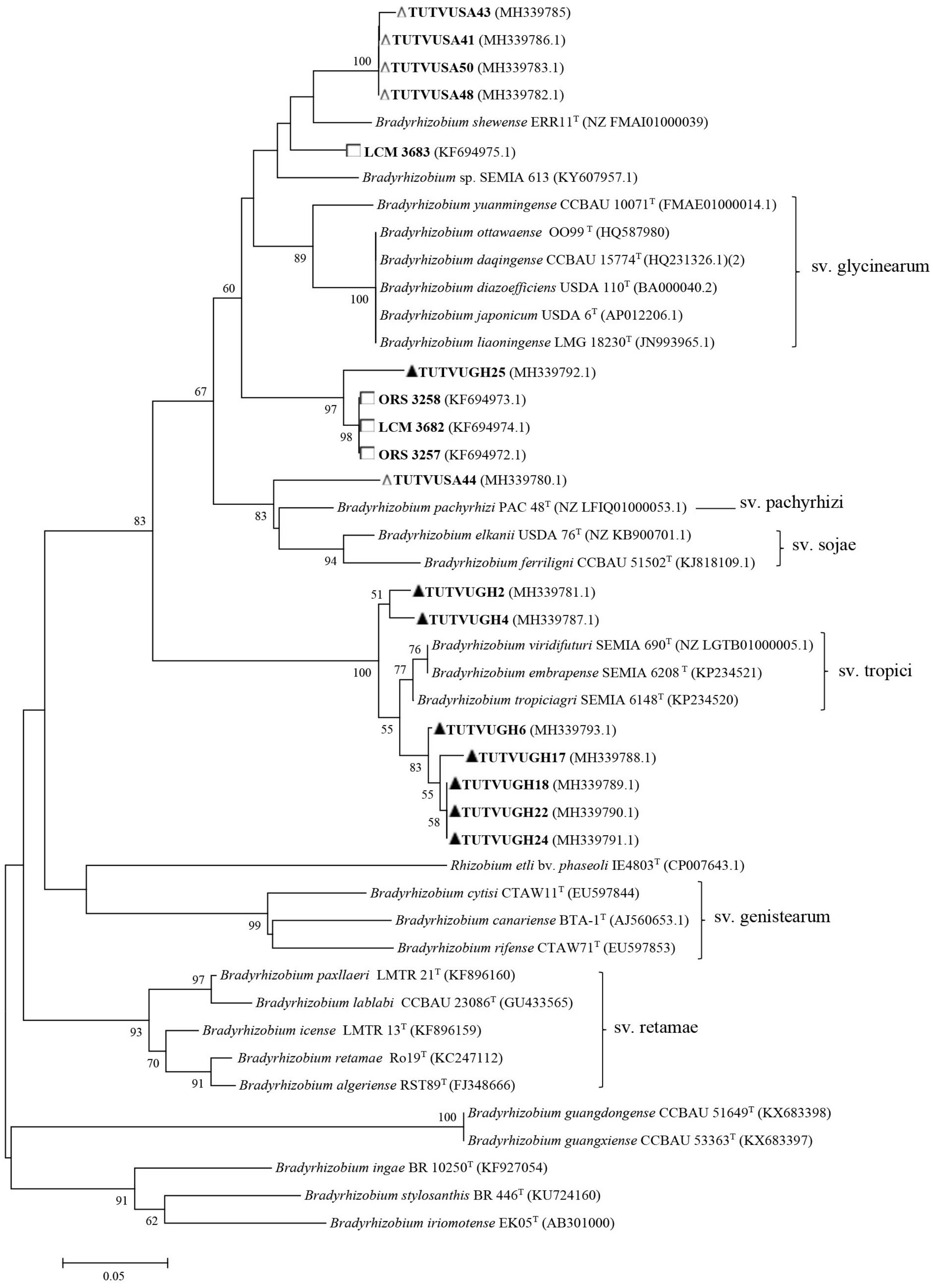

FIGURE 4 | Neighbor-joining molecular phylogenetic analysis of cowpea nodulating rhizobia from ▲Ghana, ☐ Senegal, and △ South Africa based on *nodC* sequences with type strains of *Bradyrhizobium* species. The evolutionary history was inferred by using the Neighbor-joining method based on the Kimura 2-parameter model. The scale bar indicates the number of substitutions per site. The percentage of trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. Evolutionary analyses were conducted in MEGA6.

importers of soybean in the world due to low local production, (Mutegi and Zingore, 2014).

As a legume, soybean obtains about 50–60% of its N nutrition from the atmosphere (Hardarson and Atkins, 2003; Salvagiotti et al., 2008). In Africa, N contribution by soybean is about 63 kg N ha^{-1} in Malawi (van Vugt et al., 2018), and up to 290 kg N ha^{-1} in South Africa (Mapope and Dakora, 2016).

Historically, soybean was believed to be nodulated by strains of only *B. japonicum,* which are not endemic to African soils. As a result, new soybean genotypes [Tropical Glycine cross (TGx)], were bred that would nodulate freely with *Bradyrhizobium* populations indigenous to African soils (Pulver et al., 1985; Abaidoo et al., 2000). These so-called promiscuous TGx soybean genotypes can fix more N_2 than the strict nodulating varieties from North America due to their ability to form more effective symbiosis with indigenous *Bradyrhizobium* strains in African soils (Mpepereki et al., 2000). The TGx soybean varieties also seem to have the ability to attract diverse indigenous bradyrhizobia in African soils as shown by *B. japonicum, B. diazoefficiens,* and *B. elkanii* which were recently identified as the dominant strains nodulating soybean in South Africa, Ethiopia, and Mozambique (Jaiswal et al., 2016; Naamala et al., 2016; Chibeba et al., 2017; Gyogluu et al., 2018). *B. elkanii* is also reported to be the major microsymbiont nodulating soybean in Malawian and Kenyan soils (Herrmann et al., 2014; Parr, 2014). Jaiswal et al. (2016), Naamala et al. (2016), and Gyogluu et al. (2018) have similarly found *B. elkanii* and some native *Bradyrhizobium* species to be the dominant symbionts species nodulating soybean in South Africa, Mozambique and Ethiopia. Geographically speaking, an earlier study by Abaidoo et al. (2000) also indicated that *B. elkanii* and *B. japonicum* were the most dominant bacterial symbionts isolated from root nodules of soybean in Benin, Cameroon, Ghana, Nigeria, Togo, and Uganda. Taken together, these findings from the various studies confirm the nodulation of soybean by a diverse group of bradyrhizobia, but with *B. elkanii* and *B. japonicum* being very dominant.

Poor yield of soybean when it was first introduced into new areas outside Southeast Asia, (its center of origin and domestication) was attributed to the lack of co-evolved rhizobial strains in those soils (Pulver et al., 1985; Maingi et al., 2006; Abaidoo et al., 2007; Li et al., 2010; Chianu et al., 2011; Parr, 2014; Jaiswal et al., 2016). As a result, inoculation of soybean with exotic rhizobia has been the practice when soybean is introduced into new regions. Even with the TGx soybean genotypes which can nodulate freely with indigenous rhizobia, there are instances where native strains are either ineffective or low in numbers, suggesting soybean must still be inoculated with effective strains, whether indigenous or exotic (Sanginga et al., 2000; Giller, 2001; Okogun and Sanginga, 2003; Osunde et al., 2003; Abaidoo et al., 2007; Klogo et al., 2015). Inoculation is recommended in virgin soils when there are less than 10 cells of indigenous rhizobia per gram of soil (Thies et al., 1991, 1992; Sanginga et al., 1996; Sessitsch et al., 2002; Okogun and Sanginga, 2003). A number of studies have indicated the presence of highly effective native rhizobia in African soils that can be used as inoculants for increased soybean production (Abaidoo et al., 2000, 2007; Sanginga et al., 2000; Musiyiwa et al., 2005; Tefera, 2011; Youseif et al., 2014; Klogo et al., 2015; Gyogluu et al., 2016; Chibeba et al., 2017).

GROUNDNUT NODULATION BY DIVERSE RHIZOBIAL POPULATIONS IN AFRICA

Though native to South America, groundnut is an important grain legume in Africa (Hammons, 1982), brought by Spanish and Portuguese explorers on their voyages to Africa. Due to its ability to fix N_2, groundnut has become a significant component of traditional cropping systems. The amount of N-fixed by groundnut can vary hugely depending on the genotype (Mokgehle et al., 2014) and the efficacy of the rhizobial strains involved in the symbiosis (Paffetti et al., 1998). In general, however, groundnut is known to have high N_2-fixing capacity as it can obtain about 88–93% of its N nutrition from BNF and contribute up to 206 kg N ha^{-1} in cropping systems (Boddey et al., 1990; Peoples et al., 1991; Toomsan et al., 1995; Hoa et al., 2002; Osei et al., 2018). Estimates of N contribution by groundnut was up to 188 kg N ha^{-1} in South Africa (Mokgehle et al., 2014), 58–101 kg N ha^{-1} in Ghana (Konlan et al., 2013), and 19–79 kg N ha^{-1} in Zambia (Nyemba and Dakora, 2010). Despite the agronomic importance of groundnut, studies of its microsymbionts are relatively few, and cover only four African countries, namely Cameroon (Ngo Nkot et al., 2008), Morocco (El-Akhal et al., 2008), Ghana (Osei et al., 2018), and South Africa (Law et al., 2007; Steenkamp et al., 2008; Jaiswal et al., 2017).

Whether because nodule formation in groundnut is by crack entry and infection thread invasion (Tajima et al., 2008), groundnut-nodulating symbionts tend to reveal high levels of diversity and heterogeneity when obtained from different regions of Africa. This heterogeneity could be due to the high level of promiscuity reported for groundnut nodulation (Nievas et al., 2012; Jaiswal et al., 2017; Osei et al., 2018) as it can form effective symbiosis with both slow- and fast-growing bacteria belonging to the genera *Rhizobium* and *Bradyrhizobium* in African soils (Taurian et al., 2006; El-Akhal et al., 2008; de Freitas and Silva, 2013; Jaiswal et al., 2017; Osei et al., 2018). The fast-growing rhizobia that are reported to effectively nodulate groundnut in African soils, include *R. giardinii* and *R. tropici* (Taurian et al., 2006; Jaiswal et al., 2017; Osei et al., 2018).

Based on ribosomal and symbiotic gene sequence analyses, *B. yuanmingense* and *R. tropici* were identified as the microsymbionts nodulating groundnut in Ghanaian soils (Osei et al., 2018). In South Africa, however, Jaiswal et al. (2017) also reported the presence of a huge diversity of bacteria nodulating groundnut, based on ITS-RFLP, core and symbiotic gene sequence analyses, with *Rhizobium* and *Bradyrhizobium* as the major dominants of groundnut nodulation. Of the latter, *B. pachyrhizi* and novel *Bradyrhizobium* species close to *B. guangdongense* and *B. diazoefficiens* were responsible for groundnut nodulation, while of the *Rhizobium* group, *R. tropici* and other novel *Rhizobium* species also contributed to groundnut nodulation. Clearly, the taxonomic position of rhizobia nodulating groundnut is still not well defined. These results, however, do suggest that chromosomal and symbiotic genes could have the same evolutionary history.

NODULATION OF WILD LEGUMES BY DIVERSE BRADYRHIZOBIA IN AFRICA

Besides the nodulation of economically important grain legumes, *Bradyrhizobium* species are also associated with the nodulation of wild legumes in African soils. For example, diverse photosynthetic and non-photosynthetic bradyrhizobia with distinct host-ranges have been reported in the nodulation of *Aeschynomene* species in Senegal (Nzoué et al., 2009; Molouba et al., 1999). In Senegal, effective diverse *Bradyrhizobium* sp. found in deep soil could nodulate *Acacia albida* (Dupuy and Dreyfus, 1992; Dupuy et al., 1994). The soils of the sudanean and Sahelian regions of Senegal harbor *B. elkanii and B. japonicum* as the nodulating species of the wild legumes *Pterocarpus erinaceus* and *Pterocarpus lucens* (Sylla et al., 2002). Based on amplified fragment length polymorphism (AFLP), 16S–23S rRNA, SDS-PAGE and 16S rRNA-RFLP, diverse *Bradyrhizobium* sp. nodulating various wild legume genera (*Abrus*, *Alysicarpus*, *Bryaspis*, *Chamaecrista*, *Cassia*, *Crotalaria*, *Desmodium*, *Eriosema*, *Indigofera*, *Moghania*, *Rhynchosia*, *Sesbania*, *Tephrosia*, and *Zornia*) have been identified in the arid regions of Senegal (West Africa) (Doignon-Bourcier et al., 1999, 2000). Furthermore, microsymbionts isolated from *Zornia glochidiata* in the degraded semi-arid soils of the Sahelian ecosystem were identified as *B. liaoningense, B. yuanmingense* and *B. japonicum* based on 16S–23S rRNA and *recA* gene sequence analysis (Gueye et al., 2009).

The Cape Floristic region is largely semi-arid with nutrient-poor, acidic soils (Witkowski and Mitchell, 1987; Manning and Goldblatt, 2012) that is home to many endemic papilionoid tribes such as Crotalarieae, Podalyrieae, Psoraleeae, and Indigofereae (Goldblatt and Manning, 2002; Linder, 2003; Manning and Goldblatt, 2012), which play an important ecological role in providing symbiotic N to the ecosystem (Sprent, 2009; Sprent et al., 2010, 2013). Interestingly, the nodulation of some fynbos legumes is by *Bradyrhizobium* species. Recently, Lemaire et al. (2015) identified diverse populations of *Bradyrhizobium* as the microsymbionts of Cape legumes. *B. canariense,* which is highly acid-tolerant (Vinuesa et al., 2005), was isolated from *Indigofera gracilis,* and *B. elkanii* from *Indigofera frutescens* and *Tephrosia capensis* in the Cape fynbos of South Africa.

Bradyrhizobium nodulation has been reported for *Argyrolobium rupestre* and *Argyrolobium sericeum* from the Genisteae tribe, *Leobordea pulchra*, *L. divaricate, L. lanceolate,* and *Pearsonia obovate* from the Crotalarieae tribe, as well as *Chamaecrista* from the Cassieae tribe (Beukes et al., 2016), which have their centers of divergence in Southern Africa (Polhill and VanWyk, 2005). However, this diverse group of *Bradyrhizobium* were closely related to six novel species without alignment to known reference strains. This suggests the widespread nodulation of legumes in Africa by *Bradyrhizobium* species.

Furthermore, a phylogenetically diverse group of *Bradyrhizobium* genospecies were also found to be the microsymbionts nodulating *Crotalaria*, *Indigofera*, and *Erythrina brucei* in Ethiopia (Aserse et al., 2012). In another study, diverse *Bradyrhizobium* species were the natural microsymbionts of the tree legumes *Acacia saligna, Faidherbia albida, Erythrina brucei, Millettia ferruginea,* and *Albizia gummifera* sampled from dry, hot, semi-arid to moist cold contrasting environments in Ethiopia (Wolde-meskel et al., 2004). In an earlier report, *Faidherbia albida* was the most frequently used host for trapping *Bradyrhizobium* in Africa (Odee et al., 2002). Multilocus sequence analysis later confirmed that *B. huanghuaihaiense, B. yuanmingense, B. pachyrhizi* and some novel *Bradyrhizobium* species were the natural bacterial symbionts of *Faidherbia albida, Acacia saligna, Erythrina brucei, Albizia gummifera,* and *Millettia ferruginea* in Ethiopian soils (Degefu et al., 2017). Analysis of chromosomal (*glnII, recA, gyrB,* and *dnaK*) and symbiotic (*nodA, nodC, nifD,* and *nifH*) genes of *Bradyrhizobium* obtained from wild African legumes suggested their separate evolutionary history, and that the symbiotic genes were likely to be of African origin (Beukes et al., 2016; Degefu et al., 2017).

A diverse group of *Bradyrhizobium* species close to *B. canariense*, *B. cytisi, B. rifense, B. japonicum,* and *B. elkanii* were found to nodulate *Lupinus micranthus* in Africa, however, multilocus sequence analysis and *nodC* phylogeny defined them as symbiovar genistearum (Bourebaba et al., 2016). In Algeria, *B. algeriense* could also nodulate *Retama raetam*, *Lupinus micranthus, Lupinus albus,* and *Genista numidica*, but not *Lupinus angustifolius* or *Glycine max* (Ahnia et al., 2018). In an earlier report, *B. canariense* isolated in Spain showed the ability to nodulate serradella and *Lupinus cosentinii* in South Africa (Stępkowski et al., 2005).

FACTORS INFLUENCING *Bradyrhizobium* DISTRIBUTION IN AFRICAN SOILS

Many factors are known to influence bacterial distribution in soils, which include the presence of legume host, and environmental conditions such as soil factors (Keyser and Li, 1992; Wani et al., 1995; Dakora and Keya, 1997; Paffetti et al., 1998; Zahran, 1999; Peoples et al., 2009; Abi-Ghanem et al., 2013; Vitousek et al., 2013; Puozaa et al., 2017). These factors can affect all aspects of legume nodulation and N_2 fixation which include a decrease in rhizobial survival and diversity in soils as well as their direct effect on nitrogenase activity (Serraj, 2004). Native rhizobia and bradyrhizobia easily develop adaptive mechanisms for surviving stress (Dakora, 2012), with the latter generally exhibiting better resistance than the former. So far, 52 *Bradyrhizobium* symbionts have been identified globally for their ability to nodulate the legume plants (**Table 1**). Of these, only ten (*B. algerianse, B. cytisi, B. kavangense, B. namibiense, B. subterraneum, B. retamae, B. rifense, B. ripae, B. vignae,* and *B. shewense*) have an African origin with an ability to tolerate acidic to alkaline conditions (pH 4–9) (Chahboune et al., 2011; Chahboune et al., 2012; Guerrouj et al., 2013; Grönemeyer et al., 2015a,b, 2016, 2017; Ahnia et al., 2018; Bünger et al., 2018) (see **Table 1**). It therefore appears that the physico-chemical properties of soils play an important role in influencing the diversity of bradyrhizobial community in a niche (Jaiswal et al., 2016; Ojha et al., 2017; Puozaa et al., 2017; Rathi et al., 2018).

Rhizobial strains often perform poorly when introduced into new habitats, thus implying that their symbiotic effectiveness is often adapted to environmental factors of their local niche such as soil temperature (Roughley, 1970; Zhang et al., 2003; Suzuki et al., 2014), soil pH (Botha et al., 2004; Temprano-Vera et al., 2018), soil texture (Law et al., 2007), and host-plant type (Pule-Meulenberg et al., 2010; Jaiswal et al., 2016; Puozaa et al., 2017).

Low soil pH is for example an abiotic stress that can affect growth of the legume host, the microsymbiont, and their interaction due to high concentrations of protons that have direct or indirect effects such as forming toxic trivalent ions with aluminum, and/or reducing the availability of nutritionally and symbiotically important minerals such as Ca, Mg, P, and Mo (Indrasumunar et al., 2011; Dakora, 2012; Jaiswal et al., 2018). A recent study has shown that the occurrence and abundance of diverse cowpea rhizobial populations in Kenya was influenced by soil pH (Ndungu et al., 2018), which typically affects the availability of endogenous mineral nutrients in soils.

It is believed that the host plays a dominant role in shaping the choice of bacterial symbionts for the symbiosis (Hollowell et al., 2016). Consistent with this argument, Puozaa et al. (2017) found that when seeds with different seed coat pigmentations were planted in the same hole, they attracted different bradyrhizobial genotypes. This clearly supports the view that each host plant selects specific effective bacterial symbionts over those that are less effective for its nodulation. If so, it remains to be assessed why highly effective introduced strains fail to outcompete less effective native rhizobia.

Furthermore, the results of Puozaa et al. (2017) showed that Bambara groundnut nodulation was associated with much highly diverse bradyrhizobial populations in the drier Morwe region of South Africa (where rainfall was very low) when compared to the moist Ghanaian soils. These results are consistent with the finding that more diverse bradyrhizobial populations were found in soils from the drier or less-humid environments of Africa relative to wetter regions (Law et al., 2007; Krasova-Wade et al., 2003; Grönemeyer et al., 2014).

Besides soil moisture, Mohammed et al. (2018) also reported recently that soil mineral nutrients can influence the distribution of bradyrhizobia nodulating cowpea in the soils of South Africa and Ghana. Here, the South African bacterial symbionts were highly influenced by the endogenous soil concentrations of N, P, and Na, in contrast to Ghana, where B, Mn, and Fe had a major influence in the distribution of soil bradyrhizobia.

CURRENT CHALLENGES AND FUTURE DIRECTIONS OF LEGUME ROOT NODULATION IN AFRICAN SOILS

The data collected here have strongly contributed to the growing body of knowledge on the size and efficacy of *Bradyrhizobium* populations in African soils, as well as our understanding of the evolution of this important group of microsymbionts. Africa could be a hotspot of bradyrhizobial biodiversity, a view that compels us to search for more novel bradyrhizobia in African soils in order to learn more about their biogeography. The presence of *B. yuanmingense* and *B. elkanii* in almost all the African soils studied probably suggest that strains of these species may be the most widely distributed in African soils.

Whether bradyrhizobial distribution in Africa suggests sympatric or allopatric speciation, remains to be assessed. However, it is interesting that many highly specialized endemic novel *Bradyrhizobium* species have been identified, while others present in the same niche, microclimate, and edaphic conditions, and suspected to be novel species remain to be delineated through systematic studies. That the rhizosphere environment and the host plant play a major role in the selection of the bacterial symbiont probably explains why only highly adapted indigenous bradyrhizobia often overcome introduced inoculant strains for root nodulation in legumes. So far, very few countries have been explored for the biogeography of *Bradyrhizobium* in African soils. Studies of different regions for new rhizobia and legume germplasm could lead to the discovery of novel microsymbionts that would support agricultural productivity in the continent.

AUTHOR CONTRIBUTIONS

SJ collected the references and wrote this manuscript. FD critically reviewed and revised the article.

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