

REVIEW

Pests and diseases of trees in Africa: A growing continental emergency

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Societal Impact Statement

The increasing occurrence of native and non-native pests and diseases of trees in Africa is impacting rural livelihoods, economic development, and biodiversity across the continent. Here we provide an updated and comprehensive overview of insect pests and pathogens targeting natural and planted forests in Africa, and raise awareness of this growing emergency. Data availability and limited biosecurity of some countries are limiting the ability to tackle this invasion. An improved knowledge of taxonomy, distribution, and damage caused by these organisms will be crucial for developing continent-wide strategies to manage this emergency and enhance country-level intervention capacity.

Summary

An increasing multitude of insect pests and pathogens is targeting indigenous trees of natural forests, agroforestry systems, and exotic trees in planted forests in Africa. This is raising major concerns for a continent already challenged by adaptations to climate change, as it threatens a vital resource for food security of rural communities, economic growth, and ecosystem conservation. The accidental introduction through trade of non-native species in particular is accelerating, and it adds to the damage to tree-based landscapes by native pests and diseases. Old-time and new invaders heavily impact planted forests of exotic eucalypts, pines, and acacias, and are spreading quickly across African regions. But many non-native pathogens are recently found affecting important indigenous trees. We describe the threat to African trees by providing an overview of highly relevant insect pests and diseases of indigenous and exotic trees in Africa, and discuss implications for management and future research. The implementation of an integrated and globally coordinated approach based on improved biosecurity, biological control, and tree resistance would contribute to mitigate the potentially devastating impact of these invasions on African natural resources.

KEYWORDS

Africa, agroforestry, forest health, integrated pest management, invasive species

1 | TREES ARE CRUCIAL FOR AFRICA'S FUTURE

Natural and agroecosystems of the African continent are expected to be intensely vulnerable to climate change (Wheeler & Von Braun, 2013). This may impact particularly Sub-Saharan countries, with negative cascading effects for land management and ecosystem health, food availability, and rural livelihoods (Müller, Waha, Bondeau, & Heinke, 2014; Schlenker & Lobell, 2010; Wheeler & Von Braun, 2013).

Trees, both in forests and on cropland in agroforestry settings, will play a pivotal role in the resilience and adaptation of African landscapes to these changes. Forests and tree cover on agricultural land have a vital function for the mitigation of climatic variations and carbon storage (Albrecht & Kandji, 2003; Bonan, 2008; Zomer et al., 2016). The overall forest cover in Africa is shrinking at the rate of almost 0.5% annually, due to deforestation of natural forests (FAO, 2015). Planted forests, which include production plantations, afforestation, and agroforestry, are however growing 1.3% annually, thus helping to partially reduce the overall loss of tree cover and carbon stock (FAO, 2015). The ecological and socioeconomic benefits from natural and planted forests will be increasingly crucial for Africa's capacity to face ecological and socioeconomic changes (Evans & Turnbull, 2004; Shackleton, Shackleton, Buiten, & Bird, 2007). In particular, agroforestry provides a variety of ecosystem services to smallholders in marginal lands. Planting trees moderates the effects of climatic extremes and plant pests on crops, reduces soil degradation and deforestation, and provides farmers with food, firewood, and timber (Mbow et al., 2014; Verchot et al., 2007).

In addition to trees in natural forests, both indigenous and introduced tree species are widely planted in forestry and agroforestry settings, and are crucial for the preservation of tree cover in Africa (Bennet & Kruger, 2013; Leakey et al., 2012). *Eucalyptus*, *Pinus*, *Cupressus*, and *Acacia* spp. are among the non-indigenous trees dominating industrial plantation forestry across the continent (Evans & Turnbull, 2004), while the silk tree *Grevillea robusta* (Proteaceae) is an example of an important non-indigenous tree used in small plantations and farms (Booth & Ekeleme, 2002). Indigenous African trees contribute immensely to the continent, and global, biodiversity. Africa counts some 4,500–6,000 tree species, of which 800 are documented to contribute significantly to food security (Linder, 2014; Slik et al., 2015; UNEP, 2008). The conservation of these resources will be crucial for Africa's future.

2 | BIOLOGICAL INVASIONS AND THE THREAT TO AFRICAN ECOSYSTEMS

The introduction and establishment of non-native invasive organisms are increasing globally, showing no saturation (Seebens et al., 2017), facilitated by accelerating global trade and amplified by climatic variations (Hellmann, Byers, Bierwagen, & Dukes, 2008; Meyerson &

Mooney, 2007; Westphal, Browne, MacKinnon, & Noble, 2008). The spread of invasives in newly colonized regions reduces habitat biodiversity, disrupts ecosystem functioning, and harms economic development (Simberloff et al., 2013; Walsh, Carpenter, & Vander Zanden, 2016). Invasive plant pathogens and herbivorous arthropods in particular pose a devastating threat to the integrity of natural habitats, the productivity of agricultural commodities, and the sustainability of rural economies (Fisher et al., 2012; Lovett et al., 2016).

The global spread of tree pests and diseases of both natural and planted forests is also on the rise (Boyd, Freer-Smith, Gilligan, & Godfray, 2013; Wingfield, Brouckhoff, Wingfield, & Slippers, 2015). In the United States, for instance, around 400 forest insect pests were detected during 1860 to 2006 (Aukema et al., 2010). In Europe, over 100 non-native tree pathogens were introduced in the period 1800 to 2009 (Santini et al., 2013). These introductions have the potential to trigger deep effects on ecosystem functioning and services linked to tree-based landscapes (Boyd et al., 2013; Ghelardini et al., 2017; Kenis et al., 2009). Major recent examples are the unprecedented devastation of ash trees in the North American natural and urban forests by the non-native emerald ash borer *Agrilus planipennis* (Hermes & McCullough, 2014), the widespread mortality of European ash *Fraxinus excelsior* by the ash dieback fungus *Hymenoscyphus fraxineus*, that is threatening to functionally remove the tree from landscapes (Burokiene et al., 2015), and the wave of native and non-native arthropods and pathogens that are compromising the productivity of eucalypt plantations in its non-native range, particularly in Africa (Burgess & Wingfield, 2016; Hurley et al., 2016; Wingfield et al., 2008).

Africa is increasingly susceptible to biological invasions (Paini et al., 2016; Pratt, Constantine, & Murphy, 2017). Due to vulnerable agroecosystems, weak cross border biosecurity, and limited intervention capacity, low-income countries are more prone to suffering serious impacts from biological invasions (Early et al., 2016). The accelerating introduction and spread of non-native and highly destructive arthropods and pathogens are triggering economic emergencies and local food crises. The newly introduced fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae), for example, is devastating maize resources in numerous African countries just 2 years following detection (Nagoshi et al., 2018). The cumulative economic impact of invasives in Africa is expected to exceed 1.2 billion dollars per year (Pratt et al., 2017). Considering recent and imminent introductions this prediction may be underestimated, and the total invasion cost as proportion of gross domestic product (GDP) for many African countries is among the highest globally (Paini et al., 2016). This raises the stakes for developing locally appropriate management strategies across the continent.

Cultivation of important indigenous and introduced tree species in Africa is being increasingly targeted by new and old-time invaders, which are locally disrupting the sustainability of plantation forestry, frustrating the benefits of agroforestry, and threatening the continent's biodiversity (Crous et al., 2017; FAO, 2009a; Nair, 2001; Schroth, Krauss, Gasparotto, Aguilar, & Vohland, 2000; Speight, 2014; Wingfield et al., 2008). This highlights the urgency for coordinating efforts to limit accidental introduction of these organisms and

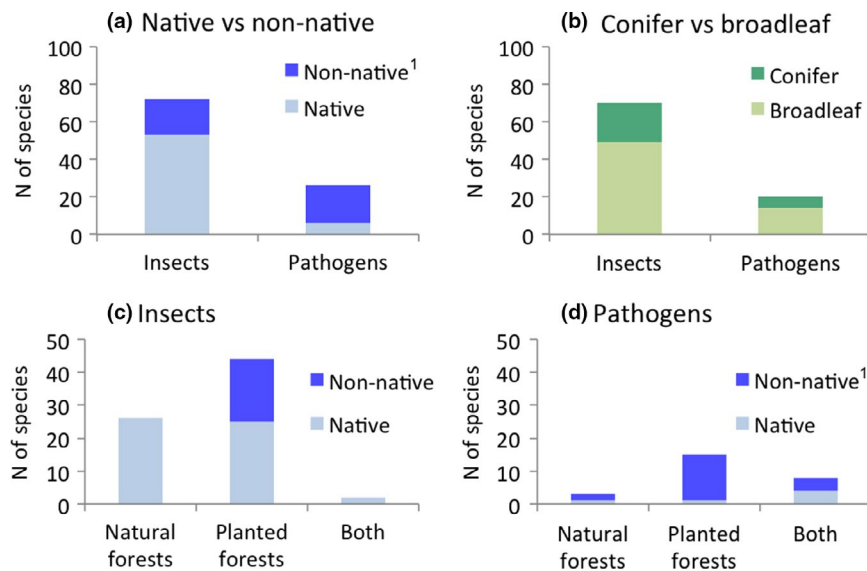


FIGURE 1 Overview of pests and diseases of natural and planted forests reported in Africa: (a) native and non-native insects and pathogens; (b) native and non-native insects and pathogens affecting conifer and broadleaf tree host; (c) native and non-native insects; and (d) pathogens targeting natural or planted forests, or both types FAO (2009a), FAO (2009b). ¹Includes pathogens of unknown origin. (Source: FAO (2009a, 2009b))

mitigate their impact (Wingfield et al., 2015). We sought to provide an overview of emerging insects and pathogens targeting trees in Africa, discuss implications for further studies and management, and raise awareness about this threat for the conservation of indigenous and introduced trees in Africa.

3 | INSECT PESTS AND PATHOGENS OF AFRICA'S TREES

Numerous native and non-native species of herbivorous insects and pathogenic microorganisms are reported to be harming indigenous and exotic trees in plantations, natural forests, and agroforestry systems across Africa. The Food and Agriculture Organization of the United Nations (FAO) (2009a, 2009b) report approximately 100 species of insects and pathogens affecting trees in planted and natural forests across northern, western, eastern, central, and southern African countries (Ghana, Kenya, Malawi, Mauritius, Morocco, South Africa, Sudan). Only half of these species are identified as native organisms, while over one third are non-native invaders, and 15% are of unknown origin. Non-native species represent over one third of insects known to damage trees, while almost two thirds of pathogens are non-native or of unknown origin (Figure 1). Broadleaf trees are affected the most, with only one third of insect and pathogen species attacking conifers. This pattern reflects the composition of native flora, constituted for the majority of broadleaves and with numerous conifers introduced as exotic plantation trees (Craib, 1947). Introduced pests and diseases are targeting for the majority planted forests, with approximately 90% of pathogens of plantation forestry being non-native or of uncertain origin. In the last few decades, new invaders have become established and spread across African landscapes, adding to the damage caused by old invaders and natives to natural and planted forests, and to indigenous and introduced tree species. The number of pests and diseases targeting plantation forestry is substantial. Over 47 native and 19 non-native defoliators,

sap-feeders, wood, and shoot borers are harming *Acacia mearnsii* (Fabaceae), *Eucalyptus* spp. (Myrtaceae), *Pinus* spp. (Pinaceae) and teak tree, *Tectona grandis* (Lamiaceae), plantations (Hurley, Slippers, Sathyapala, & Wingfield, 2017), while 15 species of pathogens are described to cause major damage to eucalypts (Wingfield et al., 2008).

We collected information on native and non-native insect pests and pathogens of trees reported in Africa using available reviews (FAO, 2009a, 2009b; Hurley et al., 2017; Nair, 2001; Roux et al., 2005; Wingfield et al., 2008), recent reports (Gichora, Kojwang, & Bosu, 2017), and invasive species compendiums to determine geographical distribution and to access additional literature (CABI, 2018; EPPO, 2014). We seek to present here a near-exhaustive updated overview of highly significant arthropods and microorganisms affecting trees in Africa based on ecological or economic impact, widespread occurrence, or recent detection.

3.1 | Native insects

An updated list of relevant native insect pests reported on indigenous and exotic trees is presented in Table 1. Coleopteran stem and seed borers, lepidopteran defoliators, stem and shoot borers, and sap-feeding hemipterans are the major groups of native pests, with several taxa affecting important indigenous trees. Among coleopterans, the seed borer *Bruchidius uberatus* (Coleoptera: Bruchidae) is a relevant pest of *Vachellia* (= *Acacia*) species (Fabaceae), and the stem borer *Sphenoptera chalcichroa* (Coleoptera: Buprestidae) is damaging *Vachellia nilotica*, an important tree of South African savannah (Atta, 1988; Delobel, 2015). The productivity of West African indigenous timber trees *Triplochiton scleroxylon* (Malvaceae), and African teak *Milicia excelsa* and *M. regia* (Moraceae), is affected by native psyllids *Diclidophlebia eastopi*, *Phytolyma fusca* (African teak gall bug), and *P. lata* (Iroko gall bug) (Hemiptera: Psyllidae), respectively (Bosu, Cobbinah, Nichols, Nkrumah, & Wagner, 2006; Ugwu & Omoloye, 2014; Wagner, Cobbinah, & Bosu, 2008a; Youmbi, Yana, & Tamesse, 2014). Among lepidopterans, the shoot borer *Orygmophora mediofoveata* (Lepidoptera: Noctuidae) is

TABLE 1 Native insect pests of indigenous and exotic trees in natural and planted forests (including agroforestry) reported in Africa

Species	Common name	Damage ^a	Tree host ^b	Host	Distribution ^c
Coleoptera					
<i>Bruchidius uberatus</i>	Seed beetle	SE	I	<i>Vachellia</i> spp.	Widespread
<i>Sphenoptera chalcichroa</i>	Silver tree borer	ST	I	<i>Vachellia nilotica</i> , <i>V. arabica</i>	SU
<i>Analeptes trifasciata</i>	Long-horned beetle	ST	I, N	<i>Tectona grandis</i> , <i>Adansonia digitata</i> , <i>Eucalyptus</i> spp.	W Africa
<i>Apate monachus</i>	Black borer	ST	I, N	<i>Azadirachta indica</i> , <i>Terminalia</i> spp., others	Widespread
<i>Apate terebrans</i>	Shot hole borer	ST	I, N	<i>Tectona grandis</i> , <i>Terminalia</i> , <i>Khaya</i> , <i>Eucalyptus</i> spp.	BE, GH, ZM
<i>Caryedon serratus</i>	Tamarind seed beetle	SE	I, N	<i>Vachellia</i> , <i>Acacia</i> , <i>Tamarindus</i> spp., others	Widespread
<i>Ellimenistes laesicollis</i>	(Weevil)	DE	I, N	<i>Eucalyptus</i> spp., <i>Grevillea robusta</i> , others	SA
<i>Hypopholis sommerii</i>	Wattle chafer	DE	I, N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Platypus cylindrus</i>	Cork oak ambr. beetle	ST	I, N	<i>Quercus suber</i>	AL
<i>Sphenoptera fulgens</i>	Root-boring beetle	ST	I, N	<i>Prosopis chilensis</i> , others	SU
<i>Chaetastus tuberculatus</i>	(Ambrosia beetle)	ST	N	<i>Eucalyptus</i> spp.	GH
<i>Colasposoma</i> spp.	(Leaf beetle)	D	N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Doliopygus</i> spp.	(Ambrosia beetle)	ST	N	<i>Tectona grandis</i> , <i>Eucalyptus</i> spp.	GH
<i>Hypothenemus</i> spp.	(Bark beetle)	ST	N	<i>Tectona grandis</i>	GH
<i>Monochelus calcaratus</i>	Wattle chafer	DE	N	<i>Acacia mearnsii</i>	SA
<i>Oemida gahani</i>	(Long-horned beetle)	ST	N	<i>Cupressus</i>	W Africa, KE
<i>Platypus lintzi</i>	(Ambrosia beetle)	ST	N	<i>Eucalyptus</i> spp.	GH
<i>Xyleborus perforans</i>	Island pinhole borer	ST	N	<i>Eucalyptus</i> spp.	GH
Hemiptera					
<i>Diclidophlebia eastopi</i>	(Psyllid)	SP	I	<i>Triplochiton scleroxylon</i>	W Africa
<i>Phytolyma fusca</i>	African teak gall bug	SP	I	<i>Milicia excelsa</i>	W Africa
<i>Phytolyma lata</i>	Iroko gall bug	SP	I	<i>Milicia regia</i>	W Africa
<i>Helopeltis anacardii</i>	(Mirid)	SP	N	<i>Eucalyptus</i> spp.	MW
<i>Lygidolon laevigatum</i>	Black wattle mirid	SP	N	<i>Acacia mearnsii</i>	SA
<i>Parasaissetia nigra</i>	Black scale	SP	N	<i>Eucalyptus</i> spp.	GH
<i>Planococcoides njalensis</i>	Cocoa mealybug	SP	N	<i>Tectona grandis</i>	GH
<i>Saissetia coffeae</i>	Hemispherical scale	SP	N	<i>Eucalyptus</i> spp.	GH
Isoptera					
Various Isoptera spp.	Termites	WO	I, N	<i>Acacia</i> , <i>Eucalyptus</i> , <i>Cupressus</i> spp.	SU, others
Lepidoptera					
<i>Anaphe venata</i>	African silk moth	DE	I	<i>Triplochiton scleroxylon</i>	GH, NI
<i>Lamprosema lateritalis</i>	Leaf tying moth	DE	I	<i>Pericopsis elata</i>	GH, MW
<i>Operophtera brumata</i>	Winter moth	DE	I	<i>Quercus afares</i>	AL, TU
<i>Orygmophora mediofoveata</i>	Shoot borer	SH	I	<i>Nauclea diderrichii</i>	W Africa
<i>Diacrisia</i> spp.	(Tiger moth)	DE	I, N	<i>Tectona grandis</i> , <i>Eucalyptus</i> spp., others	GH
<i>Gonometa podocarpi</i>	Wild silkmoth	DE	I, N	<i>Podocarpus</i> , <i>Cupressus</i> , <i>Pinus</i> , <i>Acacia</i> , <i>Eucalyptus</i>	E Africa

(Continues)

TABLE 1 (Continued)

Species	Common name	Damage ^a	Tree host ^b	Host	Distribution ^c
<i>Hypsipyla robusta</i>	Mahogany shoot borer	SH	I, N	<i>Khaya</i> , <i>Entandrophragma</i> , <i>Eucalyptus</i> spp.	E Africa, W Afr.
<i>Thaumetopoea pityocampa</i>	Processionary moth	DE	I, N	<i>Pinus</i> spp.	N Africa
<i>Achaea lienardi</i>	(Erebid moth)	DE	N	<i>Acacia mearnsii</i>	SA
<i>Ascotis selenaria</i>	Giant looper	DE	N	<i>Eucalyptus</i> spp., <i>Tectona grandis</i>	GH, NI
<i>Biston (Buzura) spp.</i>	(Looper)	DE	N	<i>Eucalyptus</i> spp.	S Africa
<i>Chaliopsis junodi</i>	Wattle bagworm	DE	N	<i>Acacia mearnsii</i>	SA
<i>Cleora herbuloti</i>	Pine looper	DE	N	<i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Coryphodema tristis</i>	Quince borer	ST	N	<i>Eucalyptus nitens</i> , <i>Malus domestica</i> , others	SA
<i>Euproctis</i> spp.	(Tussock moth)	DE	N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	GH, SA
<i>Gynanisa maia</i>	Speckled emper. moth	DE	N	<i>Acacia mearnsii</i>	SA
<i>Holocerina smilax</i>	(Emperor moth)	DE	N	<i>Pinus</i> spp.	SA
<i>Imbrasia</i> spp.	(Emperor moth)	DE	N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Narosa viridana</i>	(Slug caterpillar moth)	DE	N	<i>Eucalyptus</i> spp.	ZM
<i>Neocleosa</i> spp.	(Looper)	DE	N	<i>Eucalyptus</i> spp.	S Africa
<i>Orgyia basali</i>	(Tussock moth)	DE	N	<i>Tectona grandis</i> , <i>Eucalyptus</i> spp.	GH, NI
<i>Eutricha capensis</i>	Cape lappet moth	DE	N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Pseudobunaea irius</i>	(Emperor moth)	DE	N	<i>Acacia mearnsii</i> , <i>Eucalyptus</i> , <i>Pinus</i> spp.	SA
<i>Strepsicrathes rhotia</i>	(Tortricid moth)	DE	N	<i>Eucalyptus</i> spp.	GH
<i>Thaumetopoea wilkinsoni</i>	Processionary moth	DE	N	<i>Pinus</i> , <i>Cedrus</i> spp.	N Africa
<i>Xanthithisa tarsispina</i>	Pine looper	DE	N	<i>Pinus</i> spp.	MW
Orthoptera					
<i>Anacridium melanorhoden</i>	Sahelian tree locust	DE	I	<i>Acacia senegal</i> ; <i>Balanites aegyptiaca</i> , others	SE
<i>Manowia</i> spp.	(Eumastacidae grass-hop.)	DE	N	<i>Pinus</i> spp.	MW
<i>Phymateus kazschi</i>	(Milkweed locust)	DE	N	<i>Eucalyptus</i> spp.	GH, NI

Note: Species are arranged by insect order and origin of tree hosts (indigenous, introduced, or both). We included common name of insect species, when available, or common names of species' taxonomic group (subfamily, family, or order), in parenthesis. Sources: Nair (2001), FAO (2009a, 2009b), Gichora et al. (2017), Hurley et al. (2017), and additional sources as included in the text.

^aDamage: ST = stem borer, SE = seed borer, SP = sap feeder, DE = defoliator, SH = shoot borer, WO = wood feeder.

^bTree host: I = indigenous, N = introduced (exotic).

^cDistribution: C Africa = Central Africa, E Africa = Eastern Africa, N Africa = Northern Africa, S Africa = Southern Africa, W Africa = Western Africa, widespread = present in Northern, Eastern, Western, Central and Southern Africa, AL = Algeria, BE = Benin, GH = Ghana, MW = Malawi, NI = Nigeria, SA = South Africa, SE = Senegal, SU = Sudan, TU = Tunisia, ZM = Zambia.

a significant pest that complicates cultivation of West African timber tree *Nauclea diderrichii* (Rubiaceae), targeting young trees and seedlings in nurseries (Bosu, Acquah, & Boamah, 2018). The defoliator *Lamprosema lateritalis* (Lepidoptera: Pyralidae) is a major forest pest in Ghana and Malawi, where it causes seedling mortality on *Pericopsis elata* (Fabaceae), an endangered tree species (Atuahene & Doppelreiter, 1982; IUCN, 2018; Wagner, Cobbinah, & Bosu, 2008b).

Numerous native insect species known as pests of indigenous trees are reported to widen their host range and cause damage to

exotic trees. Long-horned beetles such as stem girdlers *Analeptes* and *Paranaleptes* spp. (Coleoptera: Cerambycidae) can cause severe damage to a wide range of indigenous trees including baobab *Adansonia digitata* and *Bombax costatum* (Malvaceae), as well as non-indigenous teak tree *T. grandis*, eucalypts, and cashew, *Anacardium occidentale* (Anacardiaceae) (Asogwa, Ndubuaku, & Hassan, 2011; Jones, 1961; Lyimo, 2017). Another native coleopteran, *Apate monachus* (Coleoptera: Bostrichidae), is a common borer affecting indigenous *Terminalia* spp. (Combretaceae) and

exotic neem tree *Azadirachta indica* (Meliaceae), while congeneric *A. terebrans* inflicts severe damage to African mahogany *Khaya* spp. (Meliaceae), and cultivated teak and eucalypts (Agboton et al., 2017; Becker, 1980). The quince borer *Coryphodema tristis* (Lepidoptera: Cossidae) is a wood borer with a wide range of native hosts, but has recently become a major pest of eucalypt plantations in South Africa (Adam, Mutanga, & Ismail, 2013). The wattle mirid *Lygidolon laevigatum* (Hemiptera: Miridae) is a major pest of the exotic black wattle, *Acacia mearnsii* (Fabaceae) in forestry plantations in South Africa, where it causes irregular branching and defoliation (Govender, 2002; Ingham, Samways, & Govender, 1998). Termites feed on wood within the wood-soil interface, and various species can locally cause severe damage to young plantings of several indigenous and exotic trees (Ambele, Bisseleua Daghela, Babalola, & Ekesi, 2018).

3.2 | Non-native insects

Numerous non-native tree pests of plantation forestry trees have invaded Africa in the past 100 years, and the accumulation of invaders has progressively increased in the last few decades (Table 2). Eucalyptus long-horned borers *Phoracantha semipunctata* and *Phoracantha recurva* (Coleoptera: Cerambycidae) are two stem borers introduced in the early 1900s in South Africa, and currently impacting eucalypt production in northern and southern African countries (Paine, Steinbauer, & Lawson, 2011). The Eucalyptus snout beetle *Gonipterus scutellatus*, the deodar weevil *Pissodes nemorensis* (Coleoptera: Curculionidae), and the teak defoliator *Hyblaea puera* (Lepidoptera: Hyblaeidae) are also historic invaders; detected in South Africa in the first half of the 20th century quickly established as important pests for eucalypts, pines, and teak, respectively (Gebeyehu & Wingfield, 2003; Hurley et al., 2017; Newete, Oberprieler, & Byrne, 2011). Non-native aphids are major pests of exotic conifers in Africa (Hemiptera: Aphididae). The pine woolly aphid *Pineus pini* and the pine needle aphid *Eulachnus rileyi* were introduced several decades ago and then spread to most regions of the continent, while the distribution of black pine aphid *Cinara cronartii* is still limited to southern Africa (Day et al., 2003; Odendaal, 1980; Zwolinski, 1990). The cypress aphid *Cinara cupressi* was introduced some 30 years ago and currently occurs in all the main cypress-growing areas, reducing the productivity of exotic cypress plantations, but also affecting native African cedar *Juniperus procera* (Cupressaceae), which natural populations in native range are declining (IUCN, 2018; Watson, Voegtlin, Murphy, & Footitt, 1999).

The wood borer *Sirex noctilio* (Hymenoptera: Siricidae), a global pest of *Pinus* spp. native to Europe, Asia, and Mediterranean Africa, was accidentally introduced and detected in South Africa in 1994, where it caused a major outbreak and tree mortality in pine plantations (Tribe & Cillié, 2004). Five new non-native pests feeding on eucalypt leaves, which included three hemipterans and two hymenopteran gall makers, were introduced from Australia to South Africa since 2002 (Bush et al., 2016). The shell lerp psyllid *Spondyliaspis* cf. *plicatuloides* (Hemiptera: Psyllidae) is the most

recent of those invaders, and is currently reported in other countries (Bush et al., 2016). Following detection, the red gum lerp psyllid *Glycaspis brimblecombei* and the bronze bug *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae) spread quickly, colonizing other countries in southern and northern Africa the former, and in southern and Eastern Africa the latter (Attia & Rapisarda, 2014; Ndela, Manyangadze, Sachisuko, Lingen, & Makowe, 2018; Saavedra, Avila, Withers, & Holwell, 2015). A similar pattern of invasion is observed for the gall makers blue gum chalcid *Leptocybe invasa* and Eucalyptus gall wasp *Ophelimus maskelli* (Hymenoptera: Eulophidae). Within a few years from first introduction to the continent, *O. maskelli* was detected in Algeria, Morocco, and Tunisia, and *L. invasa* spread to several countries in northern and Eastern Africa (Asfaw, 2018; Nyeko, Mutitu, Otieno, Ngae, & Day, 2010).

3.3 | Pathogens

Microbial pathogens of trees are increasingly affecting the health of natural and planted forests in the continent, with well-known diseases and multiple recent detections of new species in the continent (Table 3). While in many cases it is not always possible to determine the geographic origin of these organisms due to their cryptic nature, non-native pathogens have a long history in the continent. *Armillaria* root rot pathogens were introduced by early settlers in South Africa with potted plants from Europe in the 1600s (Coetzee et al., 2001). The disease was first observed decimating planted pine and eucalypt in the early 1900s and later in Eastern Africa, but is now impacting native plants in woody landscapes in South Africa and Ethiopia (Coetzee, Wingfield, & Wingfield, 2018; Gezahgne, Coetzee, Wingfield, Wingfield, & Roux, 2004; Gibson, 1960). Eucalypts are hosts of several global plant pathogens. Anthracnose caused by *Colletotrichum* spp., including widespread *C. gloeosporioides*, are a problem in eucalypt plantations and nurseries as they have wide host ranges including several fruit trees for which they are known to cause post harvest disease (Mangwende, Aveling, & Chirwa, 2018). Root rots and blights caused by *Phytophthora* spp. are an important group of emerging pathogens, as they are one of the major sources of damage to plantations and can affect indigenous trees. *Phytophthora cinnamomi* causes root rot of eucalypts in South Africa and Kenya, and basal canker of *A. mearnsii* in South Africa, but also impacts natural vegetation, such as native Proteaceae of South Africa (Brasier, 2000; Nagel, Gryzenhout, Slippers, & Wingfield, 2013). Recent surveys show an incredible diversity of *Phytophthora* taxa in the country, suggesting an imminent threat to natural ecosystems (Oh, Gryzenhout, Wingfield, Wingfield, & Burgess, 2013).

Following a similar trend to the one described for some insect pests, many pathogens of *Eucalyptus* spp. are discovered and described in important eucalypt producing countries, then are later found in other African countries. The canker causing pathogen *Teratosphaeria zuluense* was detected in South Africa and later reported also from East Africa (Gezahgne, Cortinas, Wingfield, &

TABLE 2 Non-native insect pests of indigenous and exotic trees in natural and planted forests (including agroforestry) reported in Africa

Species	Common name	Damage ^a	Year detection	Tree host ^b	Host	Distribution ^c
Coleoptera						
<i>Hylurgus ligniperda</i>	Red-haired p. bark beetle	ST	1885	N	<i>Pinus</i> spp.	SA
<i>Phoracantha semipunctata</i>	Eucalyptus long-horn. bor.	ST	1906	N	<i>Eucalyptus</i> spp.	N Africa, S Africa
<i>Phoracantha recurva</i>	Lesser Euc. long-horn. bor.	ST	1906	N	<i>Eucalyptus</i> spp.	N Africa, S Africa
<i>Gonipterus scutellatus</i>	Eucalyptus snout beetle	DE	1916	N	<i>Eucalyptus</i> spp.	E Africa, S Africa
<i>Hylastes angustatus</i>	Pine bark beetle	ST	1930	N	<i>Pinus</i> spp.	SA
<i>Pissodes nemorensis</i>	Deodar Weevil	DE	1942	N	<i>Pinus</i> spp.	SA
<i>Orthotomicus erosus</i>	Mediterr. pine engraver	ST	1968	N	<i>Pinus</i> spp.	SA
<i>Trachymela tincticollis</i>	Eucalyptus tortoise beetle	DE	1982	N	<i>Eucalyptus</i> spp.	SA
Hemiptera						
<i>Ctenarytaina eucalypti</i>	Blue gum psyllid	SP	1958	N	<i>Eucalyptus</i> spp.	KE, SA
<i>Pineus pini</i>	Pine woolly aphid	SP	1960s	N	<i>Pinus</i> spp.	E, N, S Africa
<i>Pineus boernerii</i>	Pine woolly aphid	SP	1960s	N	<i>Pinus</i> spp.	E Africa, S Africa
<i>Eulachnus rileyi</i>	Pine needle aphid	SP	1970s	N	<i>Pinus</i> spp.	C, E, N, S Africa
<i>Cinara cronartii</i>	Black pine aphid	SP	1974	N	<i>Pinus</i> spp.	SA
<i>Aonidiella orientalis</i>	Oriental yellow scale	SP	1985	N	<i>Azadirachta indica</i>	W Africa
<i>Cinara cupressi sensu lato</i>	Cypress aphid	SP	1986	I, N	<i>Cupressus</i> , <i>Juniperus</i> spp.	C, E, N, S Africa
<i>Heteropsylla cubana</i>	Leucaena psyllid	SP	1992	N	<i>Leucaena</i> , <i>Mimosa</i> spp.	E, N, S, W Africa
<i>Thaumastocoris peregrinus</i>	Bronze Bug	SP	2003	N	<i>Eucalyptus</i> spp.	E, S Africa
<i>Blastopsylla occidentalis</i>	Eucalyptus psyllid	SP	2006	N	<i>Eucalyptus</i> spp.	SA
<i>Glycaspis brimblecombei</i>	Red gum lerp psyllid	SP	2012	N	<i>Eucalyptus</i> spp.	N, S Africa
<i>Spondyliaspis cf. plicatuloides</i>	Shell lerp psyllid	SP	2014	N	<i>Eucalyptus</i> spp.	SA
Hymenoptera						
<i>Sirex noctilio</i>	Sirex Woodwasp	WB	1994	N	<i>Pinus</i> spp.	N Africa, S Africa
<i>Leptocybe invasa</i>	Blue gum chalcid	GM	2000	N	<i>Eucalyptus</i> spp.	E, N, S Africa
<i>Ophelimus maskelli</i>	Eucalyptus gall wasp	GM	2002	N	<i>Eucalyptus</i> spp.	N, S Africa
Lepidoptera						
<i>Hyblaea puera</i>	Teak defoliator	DE	Old invader	N	<i>Tectona grandis</i>	E Africa, S Africa

Note: Species are arranged by insect order and then chronologically by year of detection. Sources: Nair (2001), Wingfield et al. (2008), FAO (2009a, 2009b), Gichora et al. (2017), Hurley et al. (2017), CABI (2018) and EPPO (2014), and additional sources as included in the text.

^aDamage: ST = stem borer, SE = seed borer, SP = sap feeder, DE = defoliator, WB = wood borer, GM = gall maker.

^bTree host: I = indigenous, N = introduced (exotic).

^cDistribution: C Africa = Central Africa, E Africa = Eastern Africa, N Africa = Northern Africa, S Africa = Southern Africa, W Africa = Western Africa, SA = South Africa.

Roux, 2005). The agent of pink disease *Erythricium salmonicolor* was first described in Ethiopia on Eucalypt, then appeared in South Africa where it is now infecting indigenous forest trees including native conifer *Podocarpus* spp. (Podocarpaceae), and *Ekebergia capensis*

(Meliaceae) (Roux & Coetzee, 2005). Similarly, the canker pathogen *Chrysosporthe* spp. was first reported on Eucalyptus in South Africa, now are occurring in many countries, also affecting indigenous *Syzygium* trees (Nakabonge, Roux, Gryzenhout, & Wingfield, 2006).

Africa is also affected by global pathogens of *Pinus* spp. (Burgess & Wingfield, 2001). The agent of Sphaeropsis blight and cankers *Diplodia sapinea* was reported some 100 years ago, but is still a major threat to pine health, and able to infect other *Cupressus* spp. (Bihon, Slippers, Burgess, Wingfield, & Wingfield, 2012; Linde, Kemp, & Wingfield, 1997; Swart, Knox-Davies, & Wingfield, 1985). The agent of pitch canker *Fusarium circinatum* is among the recent invaders: detected in South Africa in 1990 affecting pine seedlings in nurseries, it caused an outbreak in pine plantation 10 years ago, and is now spreading in the country (Coutinho, Steenkamp, Mongwaketsi, Wilmot, & Wingfield, 2007). The white rot fungus *Amylostereum areolatum* is a symbiont of the wood wasp *S. noctilio*, and was introduced with its insect vector to South Africa, where it causes extensive damage to pine stands in combination with the wood wasp (Slippers, Wingfield, Coutinho, & Wingfield, 2001).

The ascomycete family Botryosphaeriaceae contains a group of relevant emerging diseases in the continent, with several species involved in novel disease complexes. *Lasiodiplodia theobromae* is a long-time known native pathogen, producing cankers on many indigenous species and eucalypts (Mohali, Burgess, & Wingfield, 2005; Roux, Coutinho, Byabashaija, & Wingfield, 2001). Non-native Botryosphaeriaceae species are causing stem cankers of *Eucalyptus* (Gezahgne, Roux, Slippers, Wingfield, & Hare, 2004; Roux et al., 2005; Slippers et al., 2004) and two other species are associated with stem cankers and major dieback to the silk tree *G. robusta* in East Africa (Njuguna et al., 2011). Some Botryosphaeriaceae species are latent pathogens infecting a wide range of hosts from planted *Pinus* spp. to indigenous *Acacia* and others, thus raising concerns on imminent diseases of important indigenous species caused by Botryosphaeriaceae (Jami, Slippers, Wingfield, & Gryzenhout, 2012; Jami, Wingfield, Gryzenhout, & Slippers, 2017). Dieback of large baobab trees was recently reported from southern Africa: various microorganisms were described to be associated with symptoms, but the causes are still uncertain (Cruywagen, Crous, Roux, Slippers, & Wingfield, 2015; Cruywagen, Slippers, Roux, & Wingfield, 2017).

4 | IMPLICATIONS, MANAGEMENT, AND FUTURE DIRECTIONS

Indigenous and exotic trees in Africa are affected by a multitude of native and non-native insect pests and microbial pathogens, with detrimental consequences for African natural and planted forests, agroecosystems, and rural communities (Crous et al., 2017; FAO, 2009a; Gichora et al., 2017; Hurley et al., 2017; Roux et al., 2005; Wingfield et al., 2015). The rate of introduction of non-natives is increasing (Figure 2). This should be considered as an emergency that adds to the effects of climate change on the continent, and calls for strategies that provide smallholders and land managers with tools to mitigate such impact quickly, and ultimately preserve the productivity of natural resources (Challinor, Wheeler, Garforth, Craufurd, & Kassam, 2007; Lobell et al., 2008). The effects of climate change on

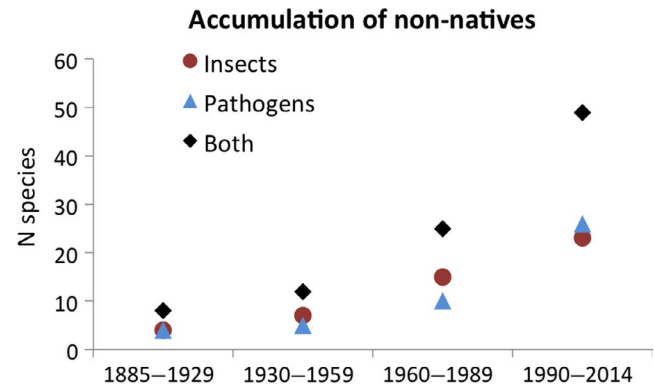


FIGURE 2 Cumulative detections of established non-native pests and diseases (and both) of natural and planted forests in Africa for the years 1900–2013. We considered detections of non-native species (or species of unknown origin) presented in Tables 2 and 3

non-natives' introduction and spread, pests and disease ecology, and ecosystem vulnerability will challenge the ability to predict their impact and implement management programs on the continent (Allen et al., 2010; Anderson et al., 2004; Dukes et al., 2009; Ramsfield, Bentz, Faccoli, Jactel, & Brockerhoff, 2016).

Invasion pathways are shaping the pattern of introduction and spread on the continent and determining taxonomy of plant hosts affected by non-native organisms. South Africa is a major port of entry for many arthropods and pathogens targeting exotic *Eucalyptus*, *Pinus*, and *Acacia* spp. in planted forests. Some non-native *Eucalyptus* pests are initially established in the southern and then northern part of Africa, but are now colonizing other regions as a result of accidental intracontinental introductions and spread. For instance, the number of *Eucalyptus* pests introduced to South Africa from other biogeographic regions surpasses the number of *Eucalyptus* pests introduced elsewhere in Africa (Faulkner, Hurley, Robertson, Rouget, & Wilson, 2017). Faulkner et al. (2017) found that eucalypt pests introduced to South Africa and then spread elsewhere in the continent are more numerous than predicted, and significantly more numerous compared to the number of pests introduced elsewhere in Africa which then spread to South Africa.

The geographic distribution of non-native pests and pathogens detection (Figure 3) may be explained by two main factors. First, the higher capacity of some country-level national plant protection organizations to detect introductions and track the spread of invasives. Secondly, the activity of local plantation forestry sectors might facilitate introductions of pests and diseases of non-indigenous trees through international exchange of improved plant material. This highlights the risk of introducing invasives through forestry and the consequences for management (Burgess & Wingfield, 2016; Wingfield et al., 2015; Wingfield, Roux, Coutinho, Govender, & Wingfield, 2001; Wingfield, Slippers, Roux, & Wingfield, 2001).

Local economic growth and increasing global trade with African countries will likely accelerate the rate of invasions further, while climate change could exacerbate invasibility and impact (Hulme, 2009; Paini et al., 2016). In this scenario, we emphasize the urgent need

TABLE 3 Pathogens of indigenous and exotic trees in natural and planted forests (including agroforestry) reported in Africa

Species	Common name	Damage ^a	Year detection	Tree Host ^b	Host species	Distribution ^c
<i>Ascomycota</i>						
<i>Lasioidiplodia theobromae</i>	-	SB, CA	-	I	<i>Boswellia</i> , <i>Eucalyptus</i> spp., other	ET, SA, UG
<i>Diplodia sapinea</i>	Sphaeropsis blight	FD, SB, CA	1912	N	<i>Pinus</i> spp.	E, S Africa
<i>Aulographina eucalypti</i>	Corky Leaf Spot	FD	1928	N	<i>Eucalyptus</i> spp.	KE, SA, ZM
<i>Fairmaniella leprosa</i>	Fairmaniella leaf spot	FD	1928	N	<i>Eucalyptus</i> spp.	SA
<i>Mycosphaerella</i> spp.	Mycosphaerella leaf blotch	FD	1935	N	<i>Eucalyptus</i> spp.	E, S Africa
<i>Kirramyces epicoccoides</i>	Phaeophleospora leaf spot	FD	1988	N	<i>Eucalyptus</i> spp.	KE, SA
<i>Teratosphaeria zuluense</i>	Coniothyrium stem canker	CA	1988	N	<i>Eucalyptus</i> spp.	ET, MA, MZ, SA, UG
<i>Chrysosporthe</i> spp.	Chrysosporthe canker	CA	1989?	I, N	<i>Eucalyptus</i> spp., <i>Syzygium cordatum</i>	KE, MA, MZ, SA
<i>Colletotrichum</i> spp.	Anthrachnose	FD	1980s	I, N	<i>Eucalyptus</i> spp., Proteaceae, other	ET, SA
<i>Fusarium circinatum</i>	Pitch canker	CA, RR	1990	N	<i>Pinus</i> spp.	SA
<i>Cylindrocladium</i> spp.	Cylindrocladium leaf blight	FD	1991	N	<i>Eucalyptus</i> spp.	KE, CO, SA
<i>Botryosphaeriaceae</i> spp.	Euc. Botryosphaeria canker	CA	1994	N	<i>Eucalyptus</i> spp.	ET, KE, SA, UG
<i>Holocryphia eucalypti</i>	Endothia canker	CA	1993	N	<i>Eucalyptus</i> spp.	SA, UG
<i>Ceratocystis fimbriata</i>	Ceratocystis wilt	CA, WI	1998	N	<i>Eucalyptus</i> spp.	CO, CT, SA, UG
<i>Ceratocystis</i> spp.	Wattle wilt	CA, WI	1990s	I, N	<i>Eucalyptus</i> spp., <i>Acacia mearnsii</i>	CO, E, S Africa
<i>Botryosphaeriaceae</i> spp.	Botryosphaeria cankers	CA	2000s	I, N	<i>Pinus</i> , <i>Acacia</i> spp.	SA
<i>Botryosphaeriaceae</i> spp.	Grevillea stem canker	CA	2001	N	<i>Grevillea robusta</i>	KE, UG
<i>Teratosphaeria gauchensis</i>	<i>Eucalyptus</i> stem canker	CA	2013	N	<i>Eucalyptus</i> spp.	KE
<i>Basidiomycota</i>						
<i>Armillaria</i> spp., <i>A. mellea</i>	Armillaria root rot	RR	1900s	I, N	<i>Eucalyptus</i> , <i>Pinus</i> spp., other TA	ET, KE, MA, SA, TA
<i>Erythricium salmonicolor</i>	Pink disease	CA	1993	I, N	<i>Eucalyptus</i> , <i>Acacia</i> , <i>Podocarpus</i>	ET, SA
<i>Quambalaria eucalypti</i>	Quambalaria blight	FD, SB	1993	N	<i>Eucalyptus</i> spp.	SA
<i>Amylostereum areolatum</i>	(symbiont of <i>Sirex noctilio</i>)	WR	1994	N	<i>Pinus</i> spp.	SA
<i>Phakopsora myrtacearum</i>	<i>Eucalyptus</i> rust	FD	2009	N	<i>Eucalyptus</i> spp.	KE, MZ, SA
<i>Puccinia psidii</i>	<i>Eucalyptus</i> rust	FD	2013	N	<i>Eucalyptus</i> spp., Myrtaceae	KE

(Continues)

TABLE 3 (Continued)

Species	Common name	Damage ^a	Year detection	Tree Host ^b	Host species	Distribution ^c
Oomycota						
<i>Phytophthora cinnamomi</i>	Phytophthora root rot	RR	1980	I, N	<i>A. mearnsii</i> , <i>Eucalyptus</i> , Proteaceae	KE, SA
<i>Pythium splendens</i>	Pythium root rot	RR	Native ^d	N	<i>Eucalyptus</i> spp.	SA
Proteobacteria						
<i>Ralstonia solanacearum</i>	Bacterial canker	CA	2000	N	<i>Eucalyptus</i> spp.	SA
<i>Pantoea</i> spp.	Bacterial canker	CA	2001	N	<i>Eucalyptus</i> spp.	SA

Note: Organisms are arranged by taxonomic group and then chronologically by year of detection. Sources: Roux et al. (2005), Wingfield et al. (2008), FAO (2009a, 2009b), Gichora et al. (2017), CABI (2018) and EPPO (2014), and additional sources as included in the text.

^aDamage: CA = canker, DI = dieback, FD = foliar disease (leaf spot, foliar blight, blotch or rust), SB = shoot blight, BR = root rot, WI = wilt, WR = white rot.

^bTree host: I = indigenous, N = introduced (exotic).

^cDistribution: C Africa = Central Africa, E Africa = Eastern Africa, N Africa = Northern Africa, S Africa = Southern Africa, W Africa = Western Africa, widespread = present in Northern, Eastern, Western, Central and Southern Africa, CO = Republic of Congo, CT = Côte d'Ivoire, ET = Ethiopia, KE = Kenya, MA = Madagascar, MZ = Mozambique, SA = South Africa, TA = Tanzania, UG = Uganda, ZM = Zambia.

^dDetected in 1994.

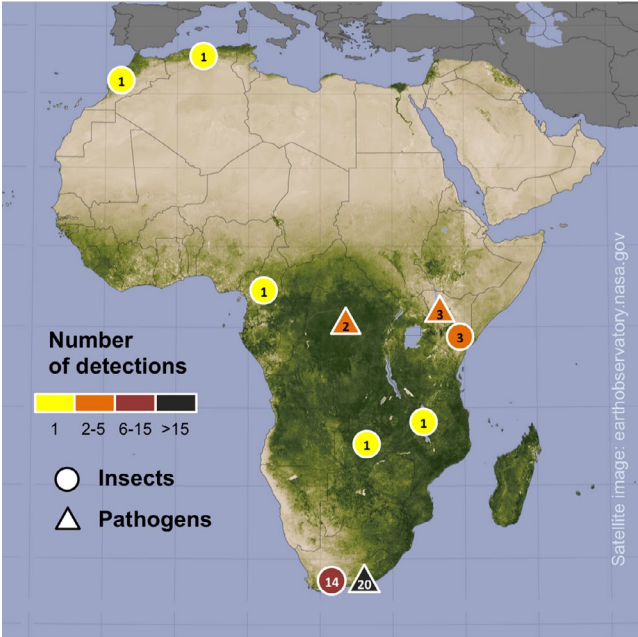


FIGURE 3 Geographic distribution of detections of non-native pests and diseases invading natural and planted forests in Africa. We considered first detections in the African continent of non-native species (or unknown origin) presented in Tables 2 and 3. (Satellite image: Africa vegetation map 2004, <https://www.earthobservatory.nasa.gov>)

for improving plant biosecurity in Africa and developing effective control options for managing invasives, but efforts require coordination at regional and international level (Burgess, Crous, Slippers, Hantula, & Wingfield, 2016; Wingfield et al., 2015). The reinforcement of phytosanitary barriers at country and regional level through improved diagnostic tools, updated plant exchange regulations, and renewed trade policies will be the key in reducing accidental introduction and spread of invasives, (Mumford, Macarthur, & Boonham, 2016; Robert, Orden, & Josling, 2004; Roy et al., 2014; Wingfield et al., 2015). Because of their cryptic nature and variable lag times, and the limited detection capacity of some countries, numerous non-native pathogenic microorganisms may have been introduced and established without discovery.

Highly efficient and long-term effective management options such as biological control, innovative silviculture practices, and selection of resistant trees could be the answer for mitigating the impact of biotic threats (Garnas, Hurley, Slippers, & Wingfield, 2012; Sollars et al., 2017; Wingfield et al., 2015; Wingfield & Swart, 1994). Biological control has been used successfully against several non-native insects (Garnas et al., 2012), and development of resistant exotic tree clones for forest plantations is promising (Oates, Külheim, Myburg, Slippers, & Naidoo, 2015; Wingfield et al., 2015). Furthermore, the opportunity for managing resistance of indigenous African tree species is worthy of attention. Relevant programs for the conservation of tree germplasm and domestication of indigenous species in Africa have been implemented, and numerous field gene banks of high-priority indigenous trees have

been deployed across African eco-regions (Dawson et al., 2014; ICRAF, 2013). Such programs offer the opportunity to evaluate the susceptibility of multiple provenances of indigenous taxa to pests and pathogens, and represent a very valuable resource for selecting resistant trees. As domestication of indigenous trees for use in agroforestry progresses, resistant varieties could be the right tool to manage emerging pests and pathogens in small plantings and farm settings.

The invasion of African natural and planted forests by biotic threats is a growing emergency of continental scale, with pervasive and long-lasting harmful effects on livelihoods and ecosystems. This is calling for action. There is a compelling need for coordinated responses at continent and international level that aim to reduce the gap in intervention capacity among African countries, consider region-specific ecological differences, and integrate innovative policy, management, and knowledge dissemination tools.

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AUTHORS CONTRIBUTION

I.G. planned and designed the manuscript, prepared tables and images, and led the manuscript preparation, I.G., M.T., J.K. and A.M. provided information included in the manuscript and contributed to writing.

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