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Review Paper

Towards a holistic understanding of non-native tree impacts on ecosystem services: A review of Acacia, Eucalyptus and Pinus in Africa

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ABSTRACT

Fast-growing, stress-tolerating tree species belonging to the genera *Acacia*, *Eucalyptus* and *Pinus* have historically been introduced to many tropical and sub-tropical regions to support various economic and environment-regulating functions. While these non-native tree (NNT) species are often highly useful, many are simultaneously invasive, generating negative environmental impacts. Current knowledge regarding the impacts of these NNTs on the ecosystem services (ES) that affect human well-being is largely informed by South African research, which inhibits a broader understanding of the contributions of these trees to those services. *Acacia*, *Eucalyptus* and *Pinus* have been widely introduced globally, yet very little is known about their contribution to ES in many locations. Here, we aimed to summarise the evidence for *Acacia*, *Eucalyptus* and *Pinus* as generating benefits and harm to ES, focusing on sub-Saharan Africa outside of South Africa. We conducted a literature search using the ISI Web of Science, which yielded 125 relevant publications. Although the three genera were reported to affect key ES in sub-Saharan Africa, the data were limited in geographic scope, with a strong bias towards East Africa as well as biases towards certain species and ecosystem service. The benefits of these NNTs relative to their costs are context dependent and may not reflect their actual impacts on ES in sub-Saharan Africa. Our review highlights the need for more systematic research from a broader perspective to manage potential conflicts and guide better management prioritisation.

1. Introduction

Globalisation has driven the introduction of thousands of non-native tree (NNT) species outside their native range (Richardson and Rejmánek, 2011), with many fast-growing and stress-tolerant trees planted to provide products such as timber and firewood, as well as benefits such as soil stabilisation (Shackleton et al., 2019) and habitat rehabilitation (Randriambanona et al., 2019). However, some introductions have fundamentally altered the composition of natural and semi-natural ecosystems (Boy and Witt, 2013), particularly where species have spread to become invasive (i.e. established self-sustaining populations in areas distant from sites of introduction; Richardson et al., 2000), displacing native biota (Hughes, 1994; Binggeli, 1996) and increasing rates of biodiversity decline (Boy and Witt, 2013). While the potential ecological damage caused by invasive NNTs is significant (Sladonja et al., 2018), the literature lacks a holistic view of the impacts of NNT species that extends beyond the ecological consequences (Tassin and Kull, 2015). To satisfy the increasing demands for the benefits provided by many NNTs without compromising biodiversity (Castro-Díez et al., 2019; Potgieter et al., 2019), there is an urgent need for research that addresses the human dimensions of invasion science (Shackleton et al., 2020).

The ecosystem services (ES) concept (Millennium Ecosystem Assessment, 2005) provides a well-established way to examine the benefits from ecosystems and the species within them from a human perspective. It encompasses the products obtained from ecosystems (provisioning services), the role of ecosystems in regulating processes such as pollination and water purification (regulating services), the nonmaterial benefits ecosystems provide as sources of recreation or spiritual inspiration (cultural services), and the services required to support production of all other services (e.g. nutrient cycling; supporting services).

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Non-native tree species provide benefits under all four ES categories. They provide products (provisioning services) to meet human needs such as timber, firewood, pulp and fodder (Castro-Díez et al., 2019), are planted for their ability to regulate local ecosystems (regulating services), including climate, by improving carbon sequestration and providing shade (Schlaepfer et al., 2020), provide aesthetic value that enhances the quality of life (cultural services) (Charles Lis and Dukes, 2007), and can enhance nutrient cycling and soil formation, increasing the productivity of non-arable land (supporting services; Hughes, 1994). However, NNT species can also generate harm under the same categories. For example, NNTs can deplete local soil nutrients and water reserves (Castro-Díez et al., 2019), or reduce agricultural productivity, resulting in income losses (Shackleton et al., 2019).

While the role of NNT species in both generating and reducing ES is widely recognised, few studies have sought to identify or estimate these impacts on a broad scale (Schlaepfer et al., 2020; van Wilgen et al., 2008). Most studies have looked at the impact of NNT species on the delivery of single ES (e.g., van Wilgen and Measey, 2020), or within single environmental contexts, seldomly addressing these impacts in the context of broader socio-ecological challenges (Charles Lis and Dukes, 2007; Vaz et al., 2017). Broad-scale studies are necessary to inform sustainable strategies for management interventions: those which will maximise the benefits while minimising the harm of NNTs to ES, considering both social and ecological factors (Egoh et al., 2020; Fastré et al., 2020; Shackleton et al., 2019). However, implementing such strategies has proven challenging (Potgieter et al., 2019). The costs and benefits of NNTs may not be measurable in absolute terms but depend on the perceptions of individuals or societal groups (Shackleton et al., 2019; Vaz et al., 2017), which can change depending on the context. Even where benefits and harm are measurable, they can arise simultaneously, with the same species generating harm to one process or societal group and benefits to another. Focusing on specific regions or single ES can provide in-depth, context-specific knowledge of the impacts of NNTs, but the benefits and harm to ES caused by NNTs in one region may not translate to those in another, inhibiting broader understanding of their impacts.

Tree species within the genera *Acacia, Eucalyptus* and *Pinus* are among the most widely planted NNT species globally (Brundu et al., 2020; Richardson et al., 2011) yet are also among the most problematic invaders (Richardson et al., 2003). They have received widespread attention in many tropical and sub-tropical regions, generating controversy and conflict (Boy and Witt, 2013; van Wilgen and Richardson, 2014). For example, many of these species serve important subsistence and commercial purposes (Potgieter et al., 2020), but can also threaten biodiversity by competing with native plant species for resources (Richardson and Van Wilgen, 2004) and reducing the services provided by those native plant species to other taxa (Pellikka et al., 2009). Research on the ecosystem processes that are affected by *Acacia, Eucalyptus* and *Pinus* in South Africa (Nel et al., 2004; Richardson et al., 1989; Richardson and Van Wilgen, 2004) has highlighted some of these potential controversies and conflicts. However, very few studies explicitly consider the negative impacts of these trees on ecosystem processes alongside the potential ecosystem service benefits they are reported to provide. Moreover, the current literature presents a geographically imbalanced view, with relatively few studies conducted outside South Africa (Piiroinen et al., 2018; Wangai et al., 2016). The overwhelming focus on South Africa in discussion of the benefits and harm to ES caused by *Acacia, Eucalyptus* and *Pinus* may result in biased generalisations that inhibit an overall understanding of their actual and context-specific effects (Pyšek et al., 2008).

This paper opens discussion of the need to present the impact of NNT species at multiple scales and to consider these impacts within multiple socio-ecological contexts. Using *Acacia*, *Eucalyptus* and *Pinus* as focal genera, we conduct a systematic literature review to summarise the evidence for the impacts of these genera on ES in sub-Saharan Africa outside of South Africa. Since 62% of rural populations across sub-Saharan Africa depend directly on ES for their livelihoods, while urban populations rely on ecosystem based resources to supplement their incomes (IPBES et al., 2018), it is likely these NNTs have some importance in generating benefits or harm to ES for the rest of sub-Saharan Africa as they do in South Africa. Yet, Africa as a continent has significant regional and sub-regional variations in biodiversity that reflect climatic differences (IPBES et al., 2018), as well as social, cultural, political, and economic predispositions unique to each country (Kueffer and Kull, 2017). Consequently, reported impacts of these NNTs in South Africa cannot be expected to be representative of the entire sub-region. Our review addresses the following three questions, and considers these in the context of socio-ecological factors known to influence both perceptions of ES and biases in the degree to which they are studied:

To what extent do the focal genera generate benefits relative to harm under each ES category across sub-Saharan Africa, and does that vary among genera?
Which ES sub-categories are reported for each genus of NNT?
Does the distribution of publications vary across sub-Saharan Africa (excluding South Africa), and are there any differences in recognition of the benefits relative to harms from NNTs among regions?

2. Methods

2.1. Focal taxa

While many genera of NNTs are both useful and problematic in sub-Saharan Africa, we focus on *Acacia, Eucalyptus* and *Pinus* as three of the most widely planted within sub-Saharan Africa and globally (Richardson et al., 2011). For example, in Ethiopia in 2011 it was estimated that *Eucalyptus* forests comprised just over 10% of all forest present (Dessie et al., 2011) and at the household scale may currently contribute up to 87% of household income (Edesa, 2021), while in 2011 *Eucalyptus* and *Pinus* accounted for nearly 40% of all stocked plantation forest (Mathu and Ng'ethe, 2011) and are among the most widely planted genera in Africa, covering 22.4% and 20.5% of all planted area, respectively (Tadesse and Fonseca, 2022). All three genera are highly speciose. Two of the genera (*Acacia* and *Eucalyptus*) are native to Australia, with some species of *Acacia* also native to other parts of the indo-pacific region (Richardson et al., 2011). *Pinus* has a native distribution strongly concentrated in the Northern Hemisphere, including North America, Europe and Asia (Richardson et al., 1994).

Countries differ in the introduction histories of these genera, and the species commonly planted. Nonetheless, as a broad generalisation, introductions began in the 1800s for timber products such as poles for construction. Through time, uses have diversified to include other products such as wood pulp, and plantings have expanded from public plantation lands to private woodlots. In some locations, species have gained important cultural value. For example, in Ethiopia species of *Eucalyptus* are widely planted in church forests (Yilma and Derero, 2020). More recently, species within these genera have been advocated as helping to solve issues of deforestation, carbon sequestration, and the restoration of soil stability and fertility, even as the negative impacts of these genera on ecosystem processes such as the regulation of hydrological and fire cycles and native biodiversity are recognised within Africa and elsewhere (Bond et al., 2019; Guedes et al., 2018).

2.2. Ecosystems services typology

We followed Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005) descriptors as far as possible, noting that supporting services are considered as ecological processes that underlie the three other categories of services (Costanza et al., 2017) and can hence be difficult to define. While use of these categories is well-established for capturing the beneficial effects of nature on people, there is ongoing discussion around how to better capture the harmful effects (Potgieter et al., 2019; Shackleton et al., 2019; Vaz et al., 2017). New typologies have been proposed to separately capture the effects of nature on people that are directly harmful, and situations where harmful effects arise due to a reduction in the ES generated. The term 'disservices' has increasingly been accepted for describing the harmful effects of nature on people, yet debate remains around how best to capture these disservices and the concept of ecosystem disservices is not as well established in the literature (Vaz et al., 2017), leading to disagreements about its use. Since our aim is to generate discussion around the potentially beneficial and harmful effects of NNTs and identify key knowledge gaps, we categorized the reported harmful impacts of these NNTs as reductions in ES, using the four ES categories (i.e., provisioning, regulating, supporting, and cultural disservices; Price, 2014; Ma et al., 2015).

2.3. Literature search

We performed a literature search on non-native/invasive species of *Acacia, Pinus*, and *Eucalyptus* in sub-Saharan Africa (excluding South Africa and overseas territories) using the ISI Web of Science on the 9th December 2020. Using the basic search tool, the search string entered was TOPIC (TS) = (Acacia OR Pinus OR Eucalyptus) **AND** (Angola OR Benin OR Botswana OR Burkina OR Burundi OR "Cabo verde" OR "Cape verde" OR Cameroon OR "Central African Republic" OR Chad OR Comoros OR Congo* OR "Cote D'ivoire" OR Dijbouti OR Guinea* OR Eritrea OR Eswatini OR Ethiopia OR Gabon OR Gambia OR Ghana OR Guinea OR Guinea-Bissau OR Kenya OR Lesotho OR Liberia OR Madagascar OR Malawi OR Mali OR Mauritius OR Mozambique OR Namibia OR Niger OR Nigeria OR Rwanda OR "Sao Tome and Prinicipe" OR Senegal OR Seychelles or "Sierra Leone" OR Somalia OR "South Sudan" OR Sudan OR Swaziland OR Tanzania OR Togo OR Uganda OR Zaire OR Zambia OR Zimbabwe) **AND** (alien OR introduc* OR exotic OR nonnative OR non-native OR invasi*).

The timespan of the search was 1990 – 2020, with 1990 chosen to align with the emergence of ideas that underpinned the Millennium Ecosystem Assessment (2005), including the Convention on Biological Diversity (1992) and the Convention to Combat Desertification (1994). We followed African country names listed in IPBES et al. (2018), accounting for name changes during that time (UK Government, 2021). Synonyms of non-native species such as "exotic", "introduced", and "alien" (Richardson et al., 2000) are interchangeably used across the literature and were integrated in the literature search. While inclusion of search terms relating to species' non-native status may have missed papers that did not consider the native/non-native status of these trees, the large diversity of native acacia species in Africa (now placed in a different genus) meant that exclusion of these terms greatly inflated the number of records retrieved. Using our search terms and the ISI Web of Science also means we may miss some regional publications or those not in English. However, as we aim to highlight biases in the global scientific literature on the impacts of NNTs, and to open discussion on the consequences of such biases, our results will nevertheless be an accurate reflection of true bias in the literature and are not intended to be exhaustive.

Assessing the effects of NNTs on ES has not been an overt focus of studies in invasion ecology (IPBES et al., 2018), so the precise terminology concerning ES was excluded from the search string. Instead, we manually identified and extracted the specific ecosystem processes impacted by these NNT genera during the data extraction stage, and classified them according to each of the four ES categories. To capture the range of ES under each category, we assigned each process to a subcategory it best described. We followed classes of the updated version (version 5.1) of the Common International Classification of Ecosystem Services (CICES; Haines-Young and Potschin-Young, 2018) as closely as possible, reverting to Millennium Ecosystem Assessment (2005) descriptors for supporting services.

2.4. Exclusion criteria

Abstracts and titles of all papers found in the online database (n = 360) were screened for relevance. An overview of the literature search process, including exclusion criteria, is summarised in Fig. 1 following methods described by Moher et al. (2009). The first round of screening excluded records ($n = 135$) if (i) studies were not based in Africa or (ii) there were no mentions of the genera of interest (i.e., *Pinus*, *Eucalyptus* or *Acacia*). A second round of screening assessed full text articles for eligibility ($n = 225$). Records were excluded ($n = 100$) where (i) the research did not mention any ES identifiable under the four MEA categories, that the focal genera impacted, (ii) the study species was of native status or (iii) the article was a review or another source of non-primary literature.

2.5. Data extraction

From all included publications ($n = 125$) we extracted the year of study, country of study, each ES process reported for any of the three NNT genera, and whether NNTs were reported as generating benefits or harm under each category, attaching these to a unique identifier for that publication (see Supplementary Material 1 for full list of publications). We assigned each country to one of four African subregions (Central, East, Southern and West) following IPBES (IPBES et al., 2018). Consistent with the tension between the benefits and harm of NNTs, we found that many papers measured the impact of NNTs on one ecosystem service in the context of another. For example, several papers examined the extent to which plantations of NNTs (where the use of a species as a plantation species would be considered as benefiting provisioning ES) led to reduced soil fertility (where a reduction in soil fertility would be considered as harming regulating ES). To capture this distinction, we recorded whether an ES set the context for the research or was the object of the study. In the example just given, a genus would be recorded as generating benefits to provisioning ES (context) but harm to regulating ES (object). Where studies explicitly measured variables that influenced the suitability of a tree species for plantation, impacts on provisioning ES were recorded as the object of the study. We did not include situations where a species or genus was only mentioned in passing as impacting an ES (for example in the discussion), since this could lead to double counting in situations where the reference used for that ES was also retrieved by and included in our literature search. We did include results obtained from either quantitative (e.g. soil analyses) or qualitative (e.g. social surveys) research.

2.6. Data analysis

Using the data extracted we: (i) summarised the abundance and geographic distribution of research in the literature and (ii) examined the frequency of benefits relative to harm of NNTs, and of provisioning, regulating, supporting and cultural service categories and associated sub-categories reported for each focal genera. The available literature will always reflect biases towards certain genera or ES for reasons unrelated to actual benefits or harm. The absolute number of reported ES among the genera provides some idea of those biases, while the frequencies of reported benefits relative to harm more explicitly examines the perceived benefits relative to the perceived costs which may inform the perceived 'net' value of that tree species/genus.

To explicitly test for differences among genera or regions in the proportion of benefits relative to harm reported in the literature, we used a generalized linear mixed-effect model (GLMM) with benefit and harm transformed into binary format (i.e., '1' for benefit, and '0' for harm) as our response variable. Either 'genus' or 'region' was included as a fixed-effect, with 'paper ID' assigned as a random effect to account for multiple datapoints extracted from the same paper. We fitted models in R (R Core Team, 2014) using the function lmer (library: LME4; Bates et al., 2015) with restricted parameters, specifying a binomial

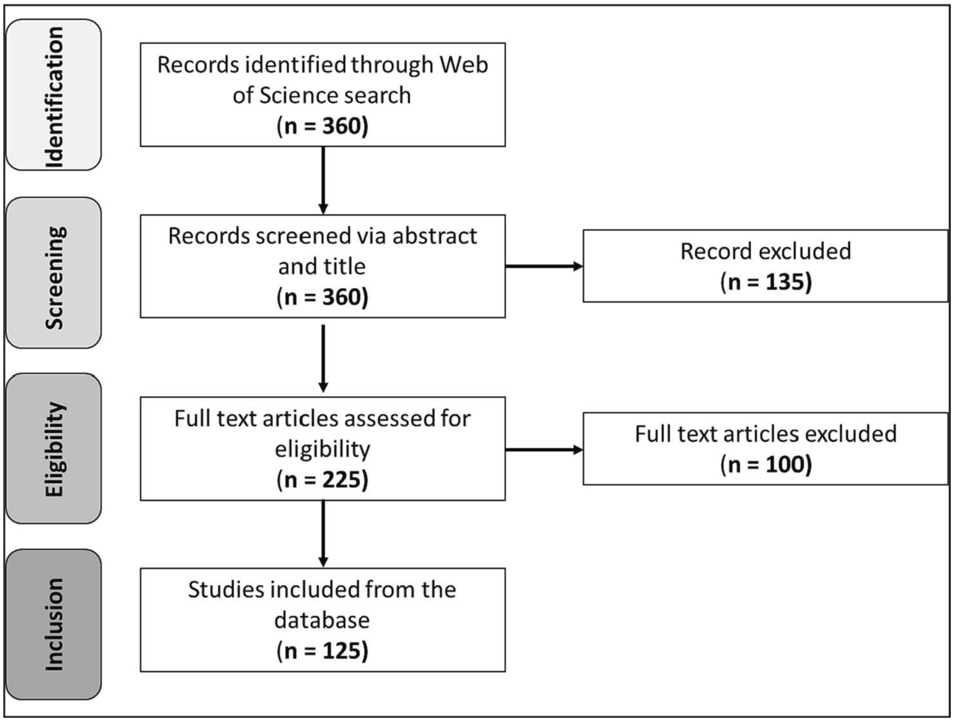

Fig. 1. PRISMA statement summarising the number of records excluded at each stage of the literature review process.

distribution. Modelled means and associated confidence intervals were extracted for the response variable.

To assess whether our predictor variables were important predictors of variation in the data, we used small-sample Akaike's information criterion (AIC_c) to measure the fit of our models relative to a null model (i.e., an intercept only model, which has no explanatory variables). The better fitting model is indicated by a smaller AIC_c value ($\Delta AIC_c = 0$), and the fit of the other model is compared against this. A difference of ≤ 2 between the best fitting model and other candidate models (i.e., $\Delta AIC_c \leq 2$) provides strong support for both models, while a difference of ≥ 2 (i.e., $\Delta AIC_c \geq 2$) provides strong support that the best fitting model has greater explanatory power (Burnham and Anderson, 2004). All calculations for AIC_c and ΔAIC_c were conducted using the R package $AIC_{C\text{-}MODAVG}$ (Mazerolle, 2020).

3. Results

3.1. Description of the data set

This review included a total of 125 publications from 1990 to 2020 that consider the benefits or harm to ES generated by *Acacia, Eucalyptus* or *Pinus*. Two studies were published in 1991, with a generally increasing trend (amid a few fluctuations) over the following two decades, with a maximum of nine papers in any given year (Fig. 2). Notably, while the search terms used retrieved 360 papers published in all sub-Saharan Africa excluding South Africa prior to review and exclusion, entering only "South Africa" in place of all other sub-Saharan African countries yielded 634 publications.

We recorded 15 sub-categories or CICES class of ecosystem services in the papers reviewed (Table 1). All 15 sub-categories were reported as an ES that benefitted from NNTs in at least one paper. Nine of the ES sub-categories were also reported as negatively impacted by NNT and were therefore considered an ES harm. Soil fertility and soil formation were two ES reported that may be considered as regulating or supporting services, depending on context and timescale (Millennium Ecosystem Assessment, 2005). In our search, NNTs were always considered as impacting soil fertility and soil formation over relatively short

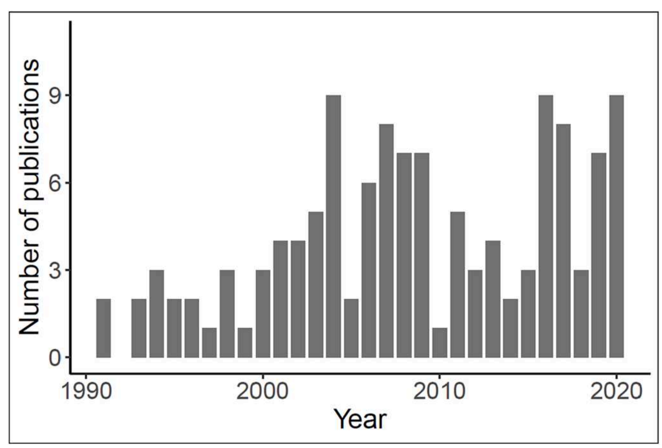

Fig. 2. The number of publications included in this review from each year (no publications were recorded in 1990).

timescales and we hence considered them as regulating services, incorporating them into the classes 'Regulation of soil quality' and 'Regulation of flows (soil)', respectively (Table 1).

Collectively, species within our three focal genera, were more frequently reported in the context of ES benefits than harm (Fig. 3), with provisioning services the most frequently reported ES category. Of the publications that examined cultural services (n = 3), all reported benefits for cultural services in the form of enhanced aesthetic value. Of the publications that examined provisioning services, over 90% reported benefits for provisioning services either when provisioning services set the context for (n = 80) or were the object of (n = 37) the study. Of those that examined regulating services, 83% considered NNTs as generating benefits when those services set the context for the study (n = 6), but only 53% of studies reported them generating benefits when they were the object of the study (n = 64). For supporting services, the benefits of NNTs to ES set the context for only 33% of studies (n = 6), and NNTs were then reported to generate a benefit to ES in around 50% studies for

Table 1
Ecosystem services reported to have been impacted by *Acacia*, *Eucalyptus* and *Pinus* species under each of the four categories recognised by the Millennium Ecosystem Assessment (MES). For provisioning, regulating and cultural services, we list the CICES class that most closely matches the subcategory extracted. For each class/sub-category, we recorded whether our focal genera were reported to generate beneficial or harmful impacts, along with a description of how we applied them to the papers we retrieved.

Sub-category	Benefit/ harm	Description
CICES class		
Provisioning		
Plants cultivated for nutrition	Benefit	Includes forage and fodder for livestock.
Plants cultivated for energy	Benefit/ harm	Cultivated plants grown as a source of energy. Includes fuelwood, firewood.
Plants cultivated for materials	Benefit/ harm	Includes trees used for construction, and to obtain tannins, wood pulp and charcoal.
Other (indirect)	Benefit	Products that are not directly obtained from the tree e.g., edible mushrooms that grow at the base.
Other (direct)	Benefit/ harm	Health products. Improving health through medicinal use or relief e.g., essential oils (benefit), allergens e.g. from pollen (harm).
Regulating		
Regulation of soil quality	Benefit/ harm	Here includes altered soil fertility e.g., through nitrogen fixation or provision of phosphorus. Also includes nutrient cycling, microbial activities and allelopathic activities.
Regulation of soil quality (carbon)	Benefit/ harm	Carbon sequestration and storage.
Regulation of flows (soil)	Benefit/ harm	Stabilisation and control of erosion rates. Here includes also soil formation following Erosion.
Regulation of flows (water)	Benefit/ harm	Regulation of water flow. Prevent or reduce surface water runoff (benefits), or increase runoff or reduce water availability (harm).
Regulation of flows (wind and sun)	Benefit	Trees planted to shield from the wind or sun.
Cultural		
Interactions with natural environment	Benefit	Improved aesthetic or ornamental purpose.
Supporting (MES sub-category)		
Biodiversity	Benefit/ harm	Restoration (benefit) or reduction (harm) of population structure and diversity of native flora, fauna and microorganisms. Invasive species included here as harm.
Fauna food	Benefit	Food source for native fauna.
Habitat	Benefit	Provision (benefit) or reduction (harm) of habit/refuge for native flora or fauna.
Primary production	Benefit/ harm	Increased (benefit) or decreased (harm) productivity of native plants or crops.

which supporting services were the object of the study (n = 53).

Question 1. To what extent do the focal genera generate benefits relative to harm under each ES category across sub-Saharan Africa, and does that vary among genera?

We recorded a total of 56 species across our three focal genera (Supplementary Material 2). Nearly twice as many publications were retrieved for *Eucalyptus* than either *Acacia* or *Pinus* (92 publications versus 48 and 44, respectively; Fig. 4A).

Across the three genera, benefits to ES were more frequently reported than harm (all estimates of the proportion of benefits to harm above 50%; Fig. 4B). Among the three genera, *Pinus* was more frequently reported as delivering ES benefits (92%) relative to harm than both *Acacia* (75%) and *Eucalyptus* (89%), with strong statistical support for this difference (a ΔAIC_c of 4.3 between the best fitting model that included genus as the predictor variable and the intercept only model; Table 2). For *Acacia,* the reduction in the proportion of benefits to harm was largely driven by studies that examined the potential for these species to invade into and compromise native vegetation.

Question 2. Which ES sub-categories are reported for each genus of NNT?

There were some differences among genera in the ES sub-categories reported to have been impacted (Fig. 5). While *Pinus* and *Eucalyptus* were considered to generate benefits to biodiversity, fauna food and habitat under supporting services, *Acacia* were overwhelmingly considered to generate benefits to primary production and only infrequently to biodiversity. Similarly, while all three genera generated benefits under at least three sub-categories of regulating services, *Acacia* was overwhelmingly associated with increased soil quality, while both *Eucalyptus* and *Pinus* were reported to generate benefits to soil carbon.

Despite some variation among genera, certain ES classes/sub-categories were frequently reported to have been impacted by all three genera. Notably, all three genera were commonly reported to generate both benefits and harm to the cultivation of plants for materials (Fig. 5). All three genera were more frequently associated with a reduction in soil quality than other sub-categories of regulating services, with all reports of *Acacia* generating harm under this category reporting a reduction in soil quality. Harmful effects on biodiversity were also frequently reported for all three genera. Notably, the classes/sub-categories for which these genera were frequently reported to generate harm were also usually the same sub-categories for which they were more frequently reported to generate benefits.

Question 3. Does the distribution of publications vary across sub-Saharan Africa (excluding South Africa), and are there any differences in recognition of the benefits relative to harms from NNTs among regions?

All sampled publications originated from only 23 out of the 46 sub-Saharan countries covered by our review (Supplementary Material 3). There was a strong bias in the geographic location of studies. Out of these 23 countries, more than half of all studies (69 papers) came from four countries: Ethiopia, Kenya, Uganda, and Congo. The former three are geographically situated in East Africa, with the majority of papers coming from countries in East Africa (78 papers; Fig. 6A).

Benefits to ES were more frequently reported than harm across the three remaining regions. However, there was some variation among regions (Fig. 6B), with a ΔAIC_c of 3.93 for the difference between a model that included 'region' as a predictor variable and an intercept-only model (i.e. there was strong support that 'region' explained a significant amount of variation in our data, Table 2). Specifically, the focal tree genera were less frequently reported as generating ES benefits relative to harm in West Africa than in both Central and East Africa.

For most sub-regions of sub-Saharan Africa, all three genera were more frequently reported as benefitting provisioning ES than other categories (Fig. 6, top row), with the notable exception of *Acacia* in Central Africa. In Central Africa, *Acacia* species were reported to generate benefits to a greater proportion of regulating services (Fig. 7). Most of the ES harms reported to be impacted by the three genera fell under the category of harms to regulating or supporting ES for most sub-regions (Fig. 7, bottom row), with harm to provisioning services reported only in East Africa.

4. Discussion

There are geographic imbalances in studies of ecosystem services within Africa and globally (Wangai et al. 2016; Egoh et al. 2020). Despite a long and global history of planting, NNT species appear to be no exception: while there is an extensive literature on the benefits and harm to ES from non-native trees in South Africa, the literature from the rest of sub-Saharan Africa is limited. We aimed to summarise the evidence for the impacts of three widely planted genera (*Acacia, Eucalyptus* and *Pinus*) on ES in the rest of sub-Saharan Africa and identify key gaps, biases and differences among regions, genera, and service categories. Our review has shown that non-native *Acacia, Eucalyptus* and *Pinus* both generate and harm ES in sub-Saharan Africa. Despite many papers reporting benefits across all four ES categories, we also recorded many examples of *Acacia*, *Eucalyptus* and *Pinus* harming ES in sub-Saharan Africa. However, there were also strong regional differences in the

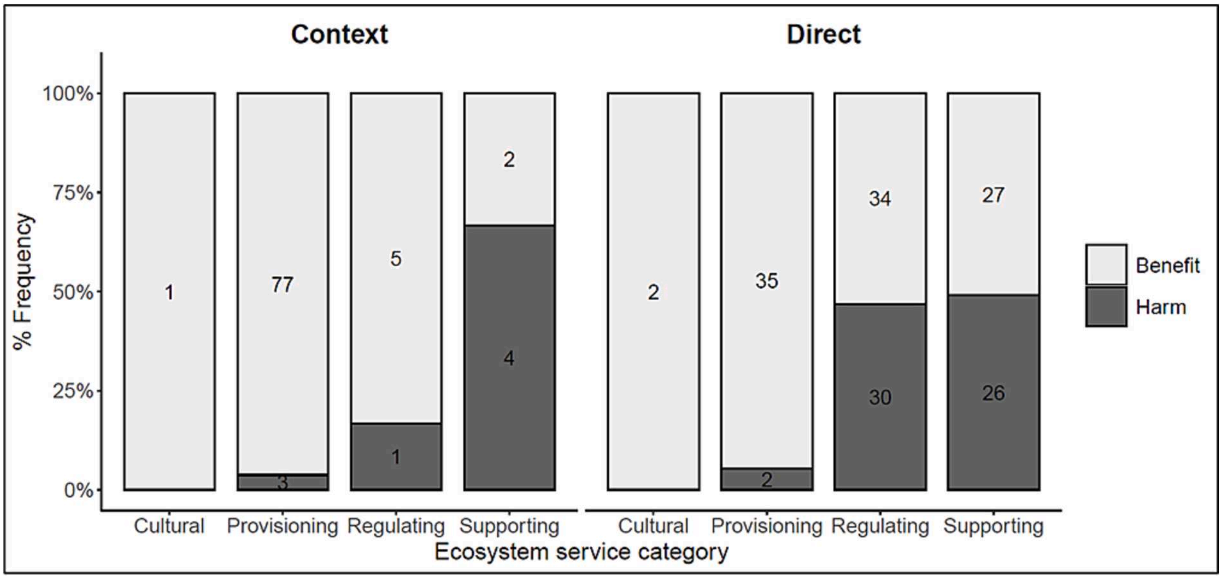

Fig. 3. Relative frequencies of publications mentioning the benefits or harm to each of the four ecosystem service categories recognised by the Millennium Ecosystem Assessment for our three focal genera (*Acacia, Eucalyptus* and *Pinus*, B). Left panel gives the proportion of publications in which ES set the context for the study, right panel gives the proportion in which the ES was the object of the study. Numbers denote total publication counts. Papers can be recorded more than once if they reported benefit or harm under multiple ES categories.

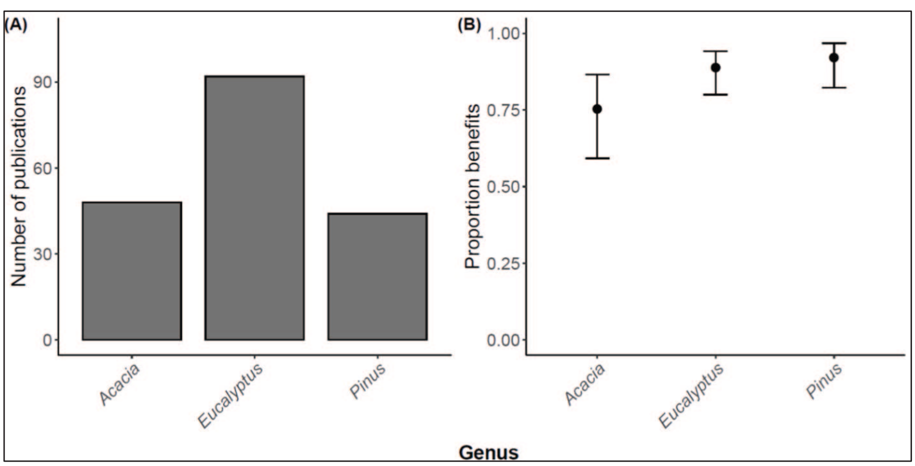

Fig. 4. The total number of publications reporting an ecosystem service impacted by each of the three focal genera (A), and the proportion of times a genus was reported to generate benefits relative to harm under each category (B). Circles represent means, bars represent 95% confidence intervals.

Table 2
Model output for linear mixed effects models examining differences in the proportion of ecosystem services relative to disservices among our three focal genera (A) and three focal regions of Africa (B). In each case, a model including either 'genus' or 'region' as a predictor variable was compared to a null, intercept only model, with ΔAIC_c values of zero indicating the better fitting of the two models. Where ΔAIC_c values between the two models ≥ 2 there is strong support for the better fitting model. *k* is the number of parameters in the model, AICc is the Akaike information criterion with correction for small sample size, and ΔAIC_c is the difference between the model AICc and the lowest AICc for the model set.

Model	*k*	Log likelihood	AIC_c	ΔAIC_c
(A) Variation among genera				
Genus	4	−220.63	449.34	0
Intercept only	2	−224.81	453.65	4.3
(B) Variation among regions				
Region	4	−151.71	313.63	0
Intercept only	2	−156.75	317.55	3.9

number of papers retrieved, and biases towards certain species and genera, as well as the ES categories considered. The varied and distinct categories of harm to ES highlighted by our review supports the need for a balanced view of NNT impacts on ES, whilst accounting for local context. Below, we examine the implications of our findings in the context of what we know about these genera more broadly, and discuss how a lack of knowledge from poorly studied and regionally specific habitats inhibits a balanced understanding of the impacts of these NNTs on ES.

4.1. The positive and negative impacts of NNTs on ecosystem processes as a source of conflict

There is much debate in the literature around how best to capture the benefits and harm to humans that arise from ecosystems. For example, while some authors propose distinct typologies to account for the direct harm to people generated by ecosystem processes (i.e. ecosystem disservices), others argue that such disservices are not isolated from

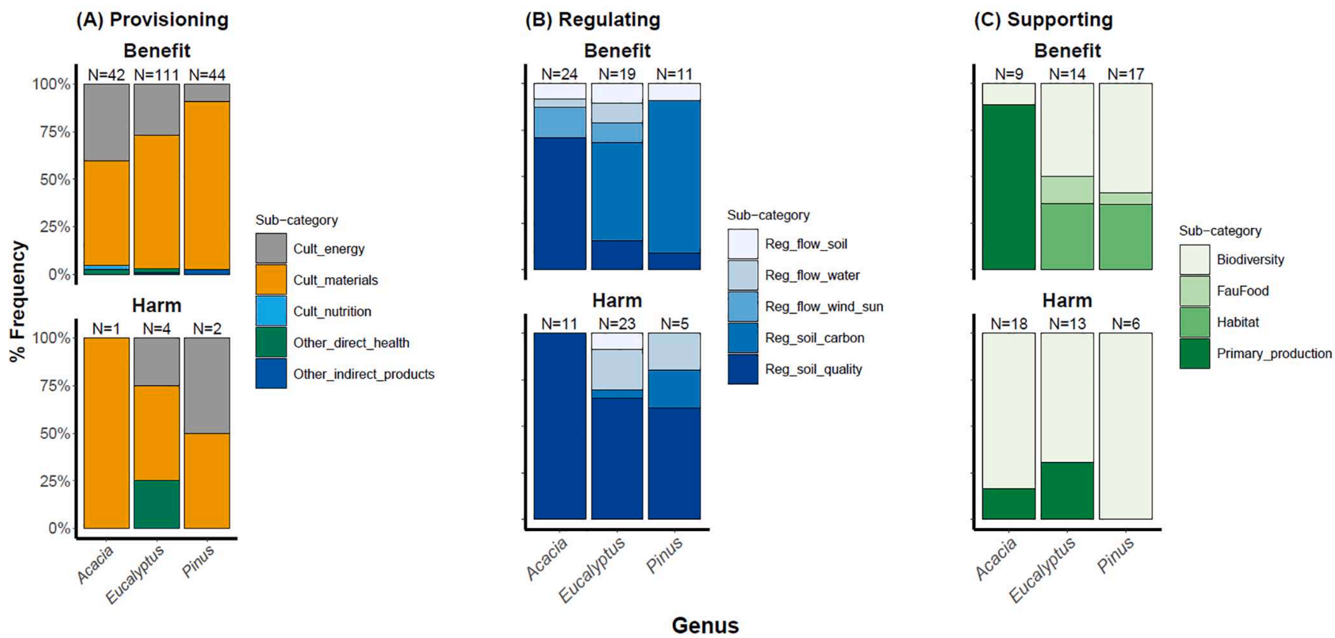

Fig. 5. Relative frequencies of reports of the benefits and harm of each of our three focal genera in each of the 16 sub-categories of provisioning (A), regulating (B) and supporting (C) ecosystem services. Cultural services (three papers only) are excluded. Numbers above bars denote the total number of publications represented by each bar. Abbreviations used as follows: Cult_energy = Plants cultivated for energy; Cult_materials = Plants cultivated for materials; Cult_nutrition = Plants cultivated for nutrition; Other_direct_health = Other (direct), here referring to plant products that benefit or harm health; Other_indirect_products = Other (indirect), here referring to secondary products from NNTs; Reg_flow_soil = Regulation of flows (soil); Reg_flow_water = Regulation of flows (water); Reg_flow_wind_sun = Regulation of flows (wind and sun); Reg_soil_carbon = Regulation of soil quality (carbon); Reg_soil_quality = Regulation of soil quality; FauFood = Fauna food. See Table 1 for further details.

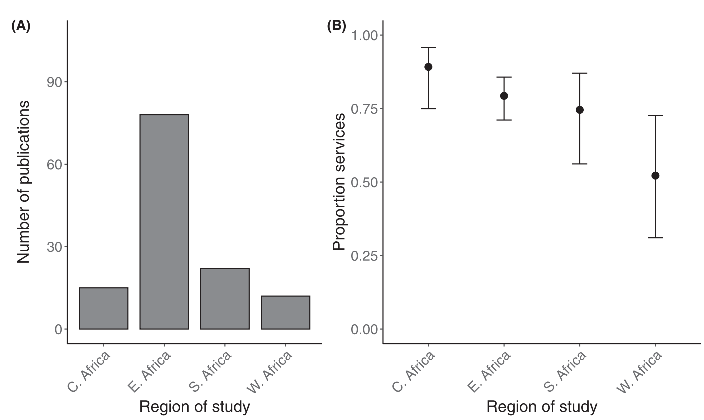

Fig. 6. The total number of publications reporting the ecosystem services impacted by each of the three focal genera in each of four regions of Africa (A), and differences among regions in the proportion of times the three focal genera were reported to generate benefits relative to harm in any of the four main ecosystem service categories (B). Circles represent means, bars represent 95% confidence intervals.

services but are supplied concurrently, a trade-off that may not be captured by separating the benefits and harm to ecosystems into dichotomous services and disservices (Saunders, 2020).

In our review, we chose to capture the potential positive and negative impacts on ecosystems processes in terms of ES provision and harm (Dickie et al., 2014), since ecological, economic and social effects are often heavily interlinked (Charles Lis and Dukes, 2007; Vaz et al., 2017). Given urbanisation trends across Africa and increasing dependence on the continued delivery of ES (IPBES et al., 2018), improved understanding of the role of these genera in mediating ES is crucial to manage the trade-offs they create (Potgieter et al., 2017; van Wilgen and Richardson, 2014). We found that although our focal NNTs generate diverse harm to ES, collectively they were more often associated with generating benefits: as in South Africa (Richardson and Van Wilgen, 2004), these NNTs have significant perceived value.

Nonetheless, difficulty in assessing trade-offs between the positive and negative aspects of these genera is that the benefits and costs reported for NNTs are determined by numerous social, cultural, economic, and ecological factors. Such factors can be very context specific (Potgieter et al., 2020; Shackleton et al., 2007). Within the same timeframe, ideas of what constitutes a harm relative to a benefit of NNTs change according to stakeholder values, affected by factors including age, gender, livelihood systems, and proximity to urban centres (Tebboth et al., 2020). Even the same interaction within a system can result in benefit or harm, depending on context (Rasmussen et al., 2017; Saunders, 2020). While the heterogeneity of reported impacts highlights conflicting societal viewpoints regarding the relative effects of these NNTs (Dickie et al., 2014), it also generates further confusion in

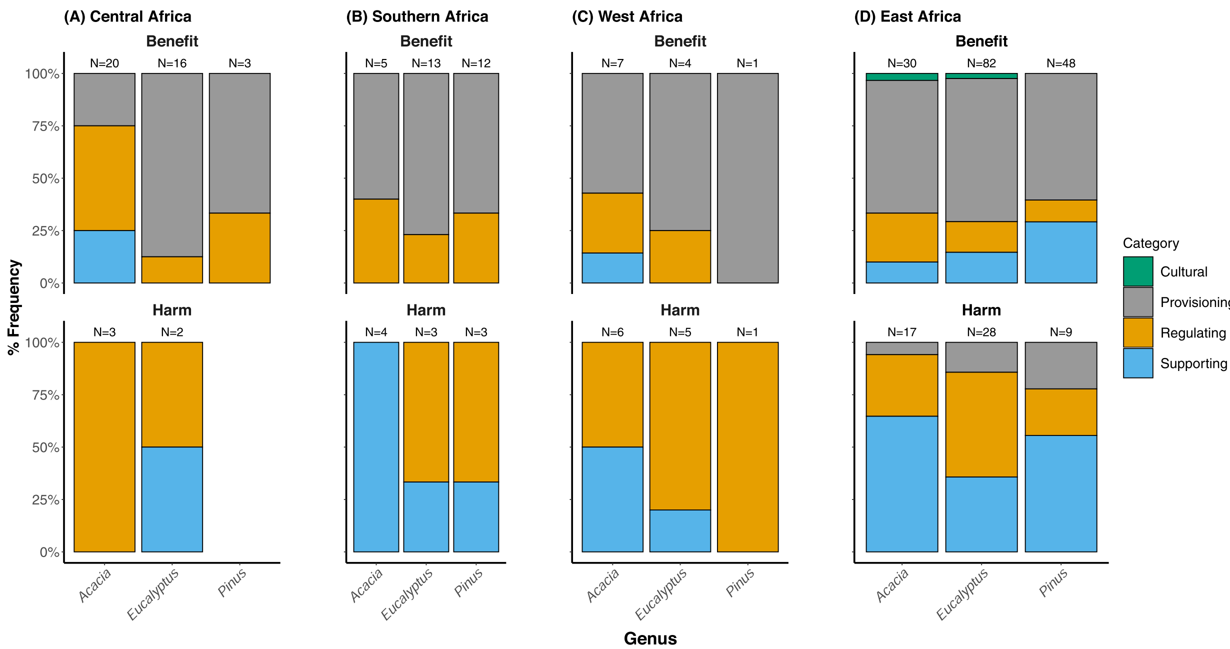

Fig. 7. Relative frequencies of each of the four ecosystem service categories reported to have been impacted by each of the three focal tree genera either via benefits (top row) or harm (bottom row) in each of the four regions of Africa covered in this review: Central Africa (A), Southern Africa (B), West Africa (C) and East Africa (D). Numbers above bars denote the total number of publications represented by each bar.

instances where the same taxa are perceived as beneficial and detrimental within a single ES category. All three genera were reported to simultaneously benefit and harm multiple ES. For example, non-native *Acacia* spp. were frequently reported to improve soil fertility through nitrogen fixation (e.g. Koutika et al., 2017; Tchichelle et al., 2017), yet a similar number of publications highlighted harm to soil quality due to *Acacia*. Moreover, in the same location, benefits to soil fertility via increased nitrogen may be offset by harm generated via a reduction of other components of soil quality, including phosphorous content.

Our review also highlights that studies of the ES impacted by NNTs are lacking at even the regional or country level in much of sub-Saharan Africa, and hence the need for a rigorous means to objectively assess the positive and negative aspects of these genera. The links between non-native species and the benefits or harm to ES are still not well-established (IPBES et al., 2018), which may, at least in part, be due to disagreements and confusion among authors in how to define negative species impacts (Blanco et al., 2022). Balancing the positive and negative aspects of these genera requires better understanding of their effects at finer scales (van Wilgen and Richardson, 2014), with explicit attention to the needs of all societal groups and sectors. Such efforts may become increasingly challenging as social and environmental contexts change (Fastré et al., 2020). For example, invasive NNTs may have increasingly negative impacts on biodiversity as they spread and become dominant, but the same species may also begin to generate important benefits if changing environmental conditions mean that native species are unable to provide important ecosystem services (Eviner et al., 2012), or if NNTs provide native species with climate 'refugia' under those changed conditions (McInerney et al., 2021). Overall, a more uniform approach to defining the positive and negative aspects of NNTs is needed (Potgieter et al., 2017), alongside a more localised understanding of ES uses and values, drawing on both qualitative insights and quantitative assessments of the distribution and impacts of NNTs.

4.2. Limitations and biases in the reviewed literature

In our review, a greater proportion of the literature reported benefits relative to harm to ES by *Pinus* than the other two genera. Information on relative benefits and harm may prove useful where decisions leading to acceptable and effective control are needed. For example, eradication efforts could focus on non-native *Eucalyptus* and *Acacia* species, whilst plantations of *Pinus* species which have high perceived benefits and lower perceived harm could be maintained and possibly replace other genera. However, it is not just the social and environmental context that are important in determining benefits and harm to ES. Optimising management decisions and evaluating the risks associated with new plantings on non-native trees is hindered by a lack of detailed knowledge of the biology and ecology of individual species (Gaertner et al., 2016; Pyšek et al., 2008), and by biases in the representation of impacts to ES by NNTs.

In addition to regional bias, our review highlighted three other sources of biases in the published literature that could affect the extent to which the literature accurately reflects the risks posed by these genera. First, within each genus there were clear biases towards certain species. Such bias could reflect the frequency with which those species are planted rather than their actual impact (Pyšek et al., 2008). For example, *Eucalyptus camuldensis, E. grandis, E. globulus and E. saligna* were species most commonly mentioned in the papers we retrieved and are also among the most widely planted in East Africa (Dessie et al., 2011). However, their popularity for planting is likely due to suitability for local environmental conditions and their growth performance, rather than consideration of potential harm to ES. Second, there were differences in the ES reported to be affected by different genera. For example, more studies reported *Eucalyptus* to harm regulating ES than to benefit them. This difference could suggest that *Eucalyptus* are more broadly harmful than beneficial, but may simply reflect that the benefits of *Eucalyptus* are widely known so that research focus has turned towards potential harm. Third, there were clear biases towards provisioning services. Such bias likely reflects the main use of these genera both at the industrial and local scale, since the primary reason for the introduction of many species was as a source of timber and fuel. Many households in Africa can generate income via home woodlots (Alemayehu and Melka, 2022), and an increase in the economic return of non-native species can enhance the perceived value of those species (Rasmussen et al., 2017). Yet, NNTs can also both generate and harm many regulating, supporting and cultural services (Dickie et al., 2011). Despite numerous benefits and harm to other ES revealed by our review, these were often represented by only a few papers.

5. Conclusion and final remarks

Tree planting is advocated as a solution to reduce deforestation, mitigate climate change, and restore ecosystems. Despite increasing recognition of the risks to ES posed by NNTs, planting continues globally. Our findings highlight that in sub-Saharan Africa, non-native *Acacia, Eucalyptus* and *Pinus* are firmly embedded in landscapes and have complex social and economic ties. Such ties can influence the degree to which societal groups recognise and perceive harm, so that while a broad range of benefits and harm to ES are recognised and reported for these genera, knowledge about their actual contributions to ES is limited and biased in many ways. Where impacts of the NNTs (both positive and negative) are described, such descriptions are often qualitative, which complicates the analyses required to inform the management of trade-offs (Potgieter et al., 2017). Quantitative measurements of benefits and harm are hindered by conceptual ambiguity in what defines a cost or benefit to humans, so that many studies within our review and in the literature more broadly (Saunders, 2020) refer to ecosystem disservices or perceived harm to ES without explicit measurement of that harm.

There is a need for a more balanced way of assessing the relative importance of ecosystems services associated with NNTs to recognise trade-offs and guide better management prioritisation in the context of future projections for both climate and invasion trajectories. Guiding management prioritisation would require a holistic approach considering the perceived benefits associated with *Acacia, Eucalyptus* and *Pinus*, whilst acknowledging both current and likely future impacts (Gaertner et al., 2016; Vaz et al., 2017). Such an approach requires detailed and accurate information on the current ES demands and supply, societal values and ecological conditions, which vary significantly across Africa (Wangai et al., 2016). While our review highlights the broad importance of these genera in sub-Saharan Africa, it also underlines the need for rigorous and systematic assessment of NNT impacts across scales. How best to balance human values and perceptions with ecological knowledge and inference at different scales remains an open question.

While we focused on sub-Saharan Africa, these genera are among the most widely planted genera in the world and the same issues, and gaps, in research we identified are likely relevant globally. As the number of non-native introductions continue to increase (Seebens et al., 2017), alongside rapid environmental and social change, efforts to achieve a more balanced understanding of the positive and negative impacts of NNTs and contextual variation in those impacts are increasingly vital.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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