Endemic darling or global change menace? A review of the woody encroacher *Leucosidea sericea* on the eastern Great Escarpment of southern Africa

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Highlights

- *Leucosidea sericea* is expanding its range and densifying.
- This leads to adverse impacts of ecosystem services such as biodiversity and water provisioning.
- Runoff-and-run-on dynamics partly modulate the spread of *Leucosidea sericea.*
- Future studies should aim to understand how the distribution of *Leucosidea sericea* responds to global environmental changes.

Abstract

Rapid woody encroachment by native species is transforming grasslands and savannas across the world. The drivers of this encroachment are diverse, complex, and potentially interlinked, including fire exclusion, overgrazing, plant-plant interactions, extirpation of local mega-fauna, carbon fertilisation, and global warming. In southern Africa, woody encroachment is a well-studied phenomenon that has primarily been documented in savanna and woodland systems, but there has been little work on woody encroachment in southern African mountain systems. These host much of the region's exceptional endemism and provide most of the region's water, and bush encroachment may have serious impacts on both. *Leucosidea sericea* Eckl. & Zeyh., is a Rosaceous shrub-tree endemic to the eastern Great Escarpment (Sneeuberg, South Africa, to Nyanga, Zimbabwe) that is believed to be rapidly expanding and densifying, however, there is very limited research on this species. Accordingly, we provide the first comprehensive review of the autecology of the species, outlining a summary of past research, and highlighting research needs related to encroachment, impact, and management. In addition, we demonstrate the potential for using repeat photography to study *L. sericea* ecology, confirming encroachment at some sites and highlighting how run-off-run-on dynamics may influence *L. sericea* establishment success. Future research on: (a) how the distribution and local density of *L. sericea* is responding to fire regimes, climate change and recent land-use changes, (b) water use of *L. sericea* to predict the potential impact of the species on water provisioning at the landscape scale, (c) insect herbivory release on *L. sericea* due to global warming, (d) changing farming practices and restoring Eland population as the original large mammal that controlled *L. sericea, s*hould be a priority to guide the management of *L. sericea*.

Keywords: Afromontane, biodiversity, fire, grassland, native invasive Ouhout, woody encroachment

1. Introduction

Mountains are biogeographically isolated "islands" of high topographic diversity, typically separated by surrounding lowlands (Spehn et al. 2011) and exhibiting high floral and faunal species diversity. Almost a third (31.6%) of the World's mountains have a larger proportion of grassland cover than forest cover and all continents except Antarctica host mountain-associated grass cover or grass-dominated biomes (de Deus Vidal et al., 2021). Montane grasslands are increasingly becoming vulnerable to global environmental changes including woody encroachment. For example, Shikangalah et al. (2020) observed that woody encroachment was widespread in mesic montane grassland systems, but has not received as much attention. Yet, close to 40% of the global population relies on these grassland systems (Grellier et al., 2013).

The process of woody encroachment is linked to ecosystem disturbance (Belay et al. 2013), and is a form of land degradation (O'Connor et al., 2014; Mokgotsi et al., 2018). For example, *Alnus alnobetula* (Ehrh.) K. Koch expansion in the Swiss Alps has caused the loss of alpine meadows and the associated grazing potential, resulting in the loss of livelihoods (Buhlmann et al., 2014). At the same time, woody plant encroachment has resulted in increased plant productivity by increasing green water flows (i.e., water stored in the soil and available for plants; Deng et al., 2021). Moreover, it has been demonstrated that bush or woody encroachment has a larger impact than climate change on water budgets in some ecosystems, an indication that the phenomenon must be considered when investigating ecosystems vulnerability to global change (e.g. drylands; Schreiner-McGraw et al., 2020).

In southern Africa, considerable attention has been given to bush encroachment in the Savanna Biome (Mucina et al., 2006), because of its adverse impacts on open-habitat sustainability, nature conservation, and rangeland-based livelihoods (Eldridge et al., 2011; O'Connor et al., 1999). It adversely affects several ecosystem services including water provision, carbon storage, nutrient cycling, grazing, and agricultural productivity (Eldridge et al., 2011). For example, it has been estimated that woody invasive alien plants reduce water flows by approximately 2.9%, 3.6%, and 19% of the mean annual naturalised runoff in South Africa, Lesotho, and eSwatini respectively (Le Maitre et al., 2016). This, in turn, affects rangeland management and water-based livelihoods of local communities for potable and productive needs (Ward, 2005; O'Connor et al., 2014; Turpie et al., 2019). Even larger impacts have been reported for grazing provisioning, with *Acacia mearnsii* (De Wild (Fabaceae) reducing grazing capacity by 72% in highly infested rangelands, and clearing thereof, increasing grazing capacity by 66% relative to densely infested sites over a 5-year period in the eastern Great Escarpment (Yapi et al. 2018). Similarly, Chikowore et al. (2021a) reported lower rangeland condition under the invasive *Robinia pseudoacacia* L. compared to uninvaded habitat in the northern Drakensberg mountains. Species such as *Colophospermum mopane* (Kirk ex Benth., Kirk ex J. Léonard, *Dichrostachys cinerea* Wight et Arn., *Senegalia mellifera* (M. Vahl) Seigler & Ebinger, *Vachellia hebeclada* (DC.) Kyal. & Boatwr. subsp. *hebeclada*, *V. karroo* (Hayne) Banfi & Galasso, and *V. tortilis* (Forssk.) Galasso & Banf (all Fabaceae), *Rhigozum trichotomum* Burch. (Bignoneaceae) are encroaching and are of major concern in both the Grassland and Savanna Biomes (Wigely et al., 2009; O'Connor et al., 2014; Shikangalah et al., 2020). However, the impacts of bush encroachment in mesic montane grasslands on biodiversity, livelihoods, and water production have not been described adequately.

Leucosidea sericea Eckl. & Zeyh. (commonly known as "old-wood" or "ouhout"), is a shrub-tree that is endemic to the eastern Great Escarpment of southern Africa, and is believed to be rapidly expanding and densifying in the grasslands of the region. The southern African Great Escarpment is a 5,000 km-long, semi-continuous mountain range system comprised of most of southern Africa's principal geological suites, in varying climatic conditions and has high floral and faunal species diversity and endemism in mountains (Clark et al., 2011). In this paper, we provide the first comprehensive review of the autecology of *L. sericea*, outlining a summary of past research, and highlighting research needs related to encroachment, impact and management. In addition, we demonstrate the potential for using repeat photography to study *L. sericea* ecology, confirming the encroachment tendency of the species and highlighting how run-off-run-on dynamics may influence *L. sericea* establishment success.

2. Material and methods

2.1 Study site

The Maloti-Drakensberg (MD) mountains form part of the southern African Great Escarpment (Mucina et al., 2006), covering c. 36,500 km^2, and has the only alpine system in southern Africa (Brand, et al., 2019; Carbutt, 2019). The MD is a grassland-dominated system (Mucina et al., 2006) that hosts rich biodiversity and endemism (Carbutt and Edwards, 2006; Neumann et al., 2014; Clark et al., 2011; Berruti, 2017; Carbutt, 2019). It is an important system for remnant populations of indigenous herbivores (especially in protected areas), including *Taurotragus oryx* (Southern Eland), *Connochaetes gnou* (Black wildebeest), *Pelea capreolus* (Grey Rhebok), *Redunca fulvorufula* (Mountain Reedbuck), and *Oreotragus oreotragus* (Klipspringer), as well as omnivores such as *Papio ursinus* (Chacma Baboon), and large predators such as *Panthera pardus* (Leopard).

The MD is a climate regulator for the region (Dedekindet al., 2016), and the most important water source for southern Africa (Taylor et al., 2016). There is a high land-use intensity in the MD, outside of protected areas, which also increases susceptibility to encroachment, and consequently land degradation is more likely to be severe outside protected areas that lack conservation and management programmes (Zeleke et al., 2009).

2.2 Methods

We carried out a scoping review based on the methodological framework outlined by Arksey and O'Malley (2005), as it enabled us to comprehensively gather, synthesise, and document knowledge gaps, and suggest future research needs on the autecology, encroachment, impact, and management of *L. sericea*. Consequently, the review process included defining the research aim, identifying relevant studies, data analysis, and reporting of results. We started with the definition of the research aim, which was to identify past research, and suggest research needs for the future, related to *L. sericea* encroachment, impact, and management. The second step was literature gathering and we conducted a literature survey from the natural sciences, to humanities, including grey literature, until 30 June 2024. In this regard, we used a search query of keywords including "*Leucosidea sericea* AND woody encroachment OR bush encroachment", "*Leucosidea sericea* AND distribution OR spatial distribution, drivers AND *Leucosidea sericea*, *Leucosidea sericea* AND management OR *Leucosidea sericea* management" to obtain information from Scopus, ScienceDirect, Web of Science, and Taylor and Francis database. Given the relative paucity of relevant literature, we also relied on institutional websites to retrieve theses and dissertations. Furthermore, we relied on popular press reports, our on-going field experiments, and our knowledge of the landscape. In addition, we leveraged on repeat photography (via rePhotoSA; adu.org.za) to document dynamics in *L. sericea* encroachment and thickening at some sites.

A total of 93 peer-reviewed academic articles were retrieved from the four bibliographic databases. Google Scholar was further used to identify any other relevant literature that might have been missed in the abovementioned databases. The next step involved title screening and removing duplicates, with 46 articles excluded in this way, while a further seven articles were removed by abstract screening. Full-text screening resulted in the exclusion of a further six articles. Using the reference lists, three articles were added to the sample. Consequently, 38 articles were considered for in-depth review, where information on *L. sericea* distribution, impact, and management was evaluated. Most of the articles that were excluded focused on pharmacology. Subsequently, we extracted data from the articles and manual coding was employed to identify key phrases and sentences. Consequently, key themes, including *L. sericea* distribution, drivers of its distribution, and impacts were explored. We did not find articles on *L. sericea* management.

3. Results and Discussion

3.1 Characterisation of selected articles

We found a total of twenty-six peer reviewed scientific articles, published in peer reviewed journals, eight theses, and three scientific reports that met our search criteria. Most of the theses were not subsequently published in journals. Relevant articles were mostly published in the *South African Journal of Botany* (six), the *African Journal of Range and Forage Science* (four), *Quaternary International* (four), *Quaternary Science Reviews* (two), *Phytoecologia* (two), and *Koedoe* (two). The rest of articles (six) came from other publications (Table 1). All these studies were conducted in South Africa and Lesotho, while no articles were found for Zimbabwe, Mozambique, or eSwatini. In addition, there were no trans-boundary studies between countries. Consequently, we speculate that countries other than South Africa and Lesotho do not have major concerns or interest in *L. sericea*. However, our review was limited to articles published in English, and could have missed articles published in Portuguese from Mozambique.

Table 1. Themes of papers, reports, chapters and theses reviewed

Themes	Study	Author
L. sericea distribution.	Descriptions of vegetation types.	Eckhardt et al. (1993), Fuls et al. (1993), Malan (1997), Eckhardt (1998), Bester (1998), Swanepoel (2007), Brand et al. (2009), Brand et al. (2011), Clark et al. (2012), van Rooyen and van Rooyen (2014), Scott-Shaw et al. (2016), Berruti (2017), Sieben et al. (2017), Bussmann et al. (2020), Daemane et al. (2022), Nsibande and Nkosi (2023a, b), Seleteng-Kose et al. (2021).
	Palaeoclimatological studies.	Lodder et al. (2018), Stewart and Mitchell (2018), Finch et al. (2021), Arthur (2022), Lennox et al. (2022), Lennox and Wadley (2022), Olatoyan et al. (2023).
Drivers of *L. sericea* distribution.	Fire, grazing. and climate studies.	Westfall et al. (1983), Vetter et al. (2006), Titshall et al. (2009), de Villiers and O'Connor (2010, 2011), de Villiers (2012), Mogashoa (2017), Lebese (2021), Turpie et al. (2021), Gwate et al. (2023).
Impacts of *L. sericea* on . ecosystem services.	Water use and community perception of degradation.	Gray et al. (2021), Ndamane et al. (2023).

Only ten papers dealing with *L. sericea* were published before 2010, while the bulk of work dealing with this species was published between 2021 and 2023 (38%; Figure 2).

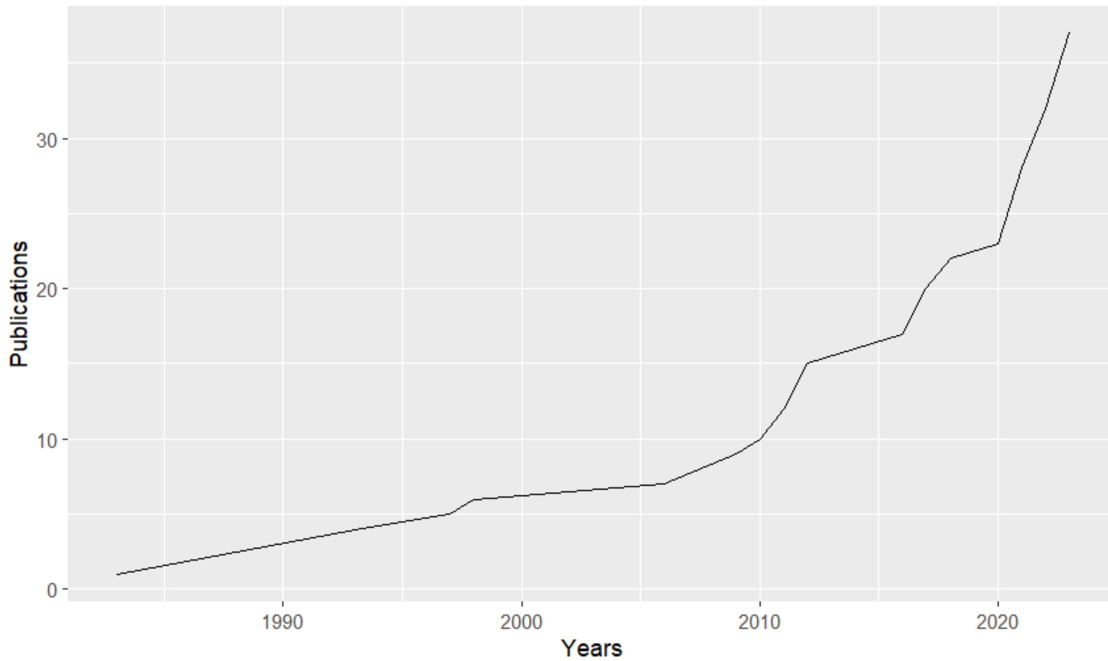

Figure 1. Number of articles published on *Leucosidea sericea* autecology, distribution, and drivers of encroachment (1983–30 June 2024).

Most of the papers (68%) focused on the distribution of *L. sericea*, through vegetation surveys and descriptions (49%) and palaeoclimatological (19%) approaches. Modelling and remote sensing studies began to emerge in *L. sericea* literature around 2017. Several articles (27%) explored mechanisms underlying *L. sericea* encroachment and densification, although few focused explicitly on *L. sericea*. These studies explored the role of disturbances such as veld fire and climate in mediating *L. sericea* occurrence. Fire-related studies started in the 1980s, continuing to 2024, but the role of climate change has only been recently amplified since 2011. Only two articles (5%) were related to *L. sericea* impacts on ecosystem services, and we did not find articles related to its management. This suggests that impacts of *L. sericea* on the ecosystem such as biodiversity may not have been described adequately to generate authoritative information to guide sustainable management of the species, hence, future research in this direction may be pertinent.

3.2 Distribution and autecology of *Leucosidea sericea*

Leucosidea sericea is endemic to southern Africa, being confined to the eastern Great Escarpment – from the Sneeuberg (Eastern Cape, South Africa) north to Nyanga (Zimbabwe; there are no confirmed records from Mozambique) – and the adjacent South African Highveld (Clark et al., 2017; Mafole et al., 2017). It has been recorded from seven provinces in South Africa (Eastern Cape, Free State, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, Northwest), and the Kingdoms of Lesotho and eSwatini (see Plate 1a). *Leucosidea sericea* grows to 2–9 m tall and occurs between 1610–2400 m elevation (Nair et al., 2012), although we have observed it at ~ 2800 m in the MD (Figure 2). The leaves are densely clustered, with serrated grey-green to silvery leaflets with silky hairs (Nair et al., 2012) (Plate 1(b)), and most closely resembles another typical Afromontane Rosaceous genus *Alchemilla* (although *Leucosidea* and *Alchemilla* occur in different tribes in Rosaceae). *Leucosidea sericea* produces small yellow flowers borne in racemes, between August and December, and is a prolific seed producer. Seeds are produced between July and November, and embedded in an old hypanthium. Flowers produce nectar and are bee-pollinated (Belay et al., 2013; Sehlakgwe and Prinsloo, 2018). It is a fire-adapted species, with burnt trees typically resprouting from the base (de Villiers and O'Connor, 2011), and the seeds require fire to germinate (Sehlakgwe and Prinsloo, 2018). *Leucosidea sericea* prefers moist environments – notably riparian environments – and areas of land disturbance (Nair et al., 2012).

Plate 1(a). *Leucosidea sericea* encroachment in the Maloti-Drakensberg, southern Africa: (A) Witsieshoek area (Batlokoa Traditional Authority), (B) Cathedral Peak Catchment IX (uKhahlamba-Drakensberg Park). Photos: M. Dlomu.

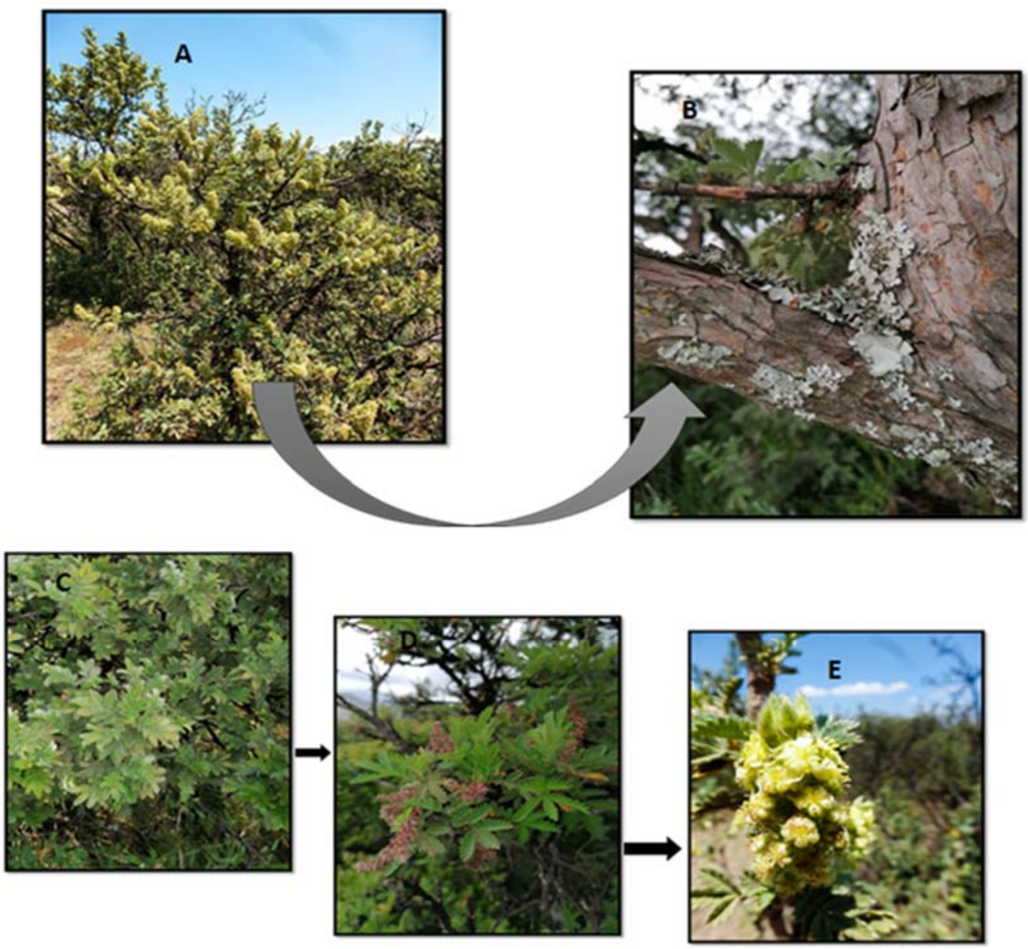

Plate 1(b). *Leucosidea sericea* (Rosaceae): (A) full plant; (B) bark; (C) foliage; (D) flowers in a raceme; (E) senescent flowers on shrub. Photo: M. Dlomu (A–D), V.R. Clark (E)

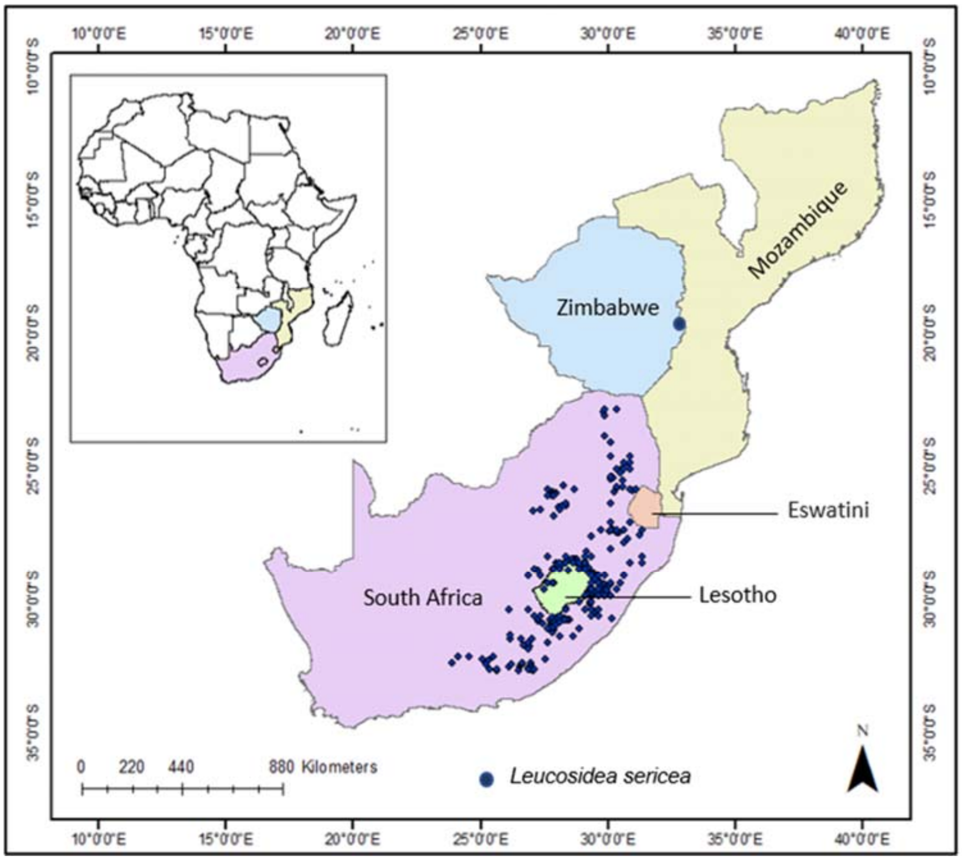

Figure 2. *Leucosidea sericea* distribution in southern Africa. Global Biodiversity Information Facility (GBIF) Occurrence Download https://doi.org/10.15468/dl.czvxwt, accessed 22 July 2021.

Leucosidea is a monotypic genus, i.e., with only one species, *L. sericea*. It was first described by Christian Friedrich Ecklon and Karl Ludwig Philipp Zeyher in 1836 (de Villiers and O'Connor, 2011; Nair et al., 2012). '*Leucosidea*' refers to the 'white' appearance of the trees (from Greek), and '*sericea*' refers to the silky appearance of the leaves (from Latin) (Plate 1 (b). The English and Afrikaans names 'old-wood' and 'ouhout' refer to the twisted stems and flaky bark (Plate 1(b)).

Although the *Rosaceae* family occurs globally, and comprises of over 100 genera and nearly 3000 species (Soundararajan et al., 2019), *L. sericea* has only one close relative in Africa, viz. the monotypic *Hagenia abyssinica* J.F. Gmel) (Zhang et al., 2017; Potter et al., 2007). *Hagenia abyssinica* is confined to the eastern tropical Afromontane Forest and sub-alpine heath from the Nyika Plateau north to Ethiopian Highlands. However, compared to *L. sericea*, *H. abyssinica* can grow up to 30 m in height (see Supplementary Material Plate 1, SP1), and its flowers are borne on large pendulous racemes (SP1). These two taxa occur in the same relatively small subtribe *Agrimonieae*, (Zhang et al., 2017), with the monotypic *Spenceria* (*S. ramalana*, Himalayas) being basal to these two species and *Agrimonia* (Zhang et al., 2017; Potter et al., 2007).

Although Zhang et al. (2017) and Potter et al. (2007) differ in terms of broader relationship circumscription, there is consensus that *Polylepis* (with 28 species, all endemic to the Andes mountains of South America) and *Cliffortia* (highly radiated in the south-western Cape and also a typical Afromontane genus Weimarck, 1941; Soundararajan, et al., 2019; Whitehouse, 2021), are relatively close woody relatives of *L. sericea* (Zhang et al., 2017; Potter et al., 2007). Other indigenous Rosaceae that are common in Afromontane environments (*sensu* White, 1981, including the Afro-alpine *sensu* definition summaries by Carbutt and Edwards, 2015, and de Deus Vidal and Clark, 2020,) are *Alchemilla*, *Cliffortia*, *Geum*, *Prunus*, and *Rubus* (Phillipson, 1987). Like *L. sericea*, some species of *Alchemilla* and *Cliffortia* form dominant woody communities (Pooley, 1993), with the potential to transform montane grasslands into woody systems as they are showing signs of range expansion (Clark et al., 2014).

Studies on *L. sericea* have often focused on the species' traditional medicinal and economic uses (Letšela et al., 2002; Nair et al., 212; Sharma et al., 2014). However, other than use for medicinal and traditional purposes, there is little published on *L. sericea*. As with other 'problematic' species – such as Australian *Acacias* - there are also benefits associated with *L. sericea*. For example, *L. sericea* plays a crucial role in traditional medicine for local communities - in South Africa, Zulu people use a paste from crushed leaves of *L. sericea* to relieve severe eye inflammation (Mafole et al., 2017). In Lesotho, *L. sericea* is a valuable commodity in the local subsistence economy as the most-preferred species at firewood markets (see Letšela et al., 2002; Letšela et al., 2003), possibly due to its slow-burning properties. The wood of *L. sericea* is also used as fence poles in areas that are permanently waterlogged (Mafole et al., 2017). Although the expansion of *L. sericea* may arguably pose a threat to the environment, the shrub remains important economically.

Most studies on the distribution of *L. sericea* have been undertaken in the MD, providing valuable insights into the social-ecological system. However, there is a dearth of studies from elsewhere where the species is known to occur. Therefore, to provide a holistic picture of the autecology and distribution of *L. sericea*, there is an urgent need to undertake studies in other areas of its distribution range to the north and south of the MD. There were also few cross-boundary studies, yet such studies could be critical in improving knowledge on the species and its management.

3.2.1 *Leucosidea sericea* encroachment in the Afromontane region

There is a dearth of studies examining *L. sericea* range dynamics. However, there is consensus among farmers and grassland ecologists (Titshall et al. 2009; de Villiers and O'Connor, 2011; Turpie et al., 2019; Turpie et al. 2021) that *L. sericea* is encroaching in the grasslands of the eastern Great Escarpment of southern Africa. In the absence of plentiful published literature, repeat photography can be useful for tracking vegetation change (Hoffman et al., 1990; Ward et al., 2014). Photographs from the repeat photography project "rePhoto" (Plant Conservation Unit, University of Cape Town) show evidence of encroachment in the Eastern Cape and KwaZulu Natal Provinces over a 73-year-period (Plate 2 and Plate 3), particularly into the mesic grasslands and along drainage lines. Consequently, there is a shift in the tools used to studying *L. sericea*. Whilst this shift in tools used is commendable, it will be prudent to combine modelling and ground based studies to better track dynamics in *L. sericea*.

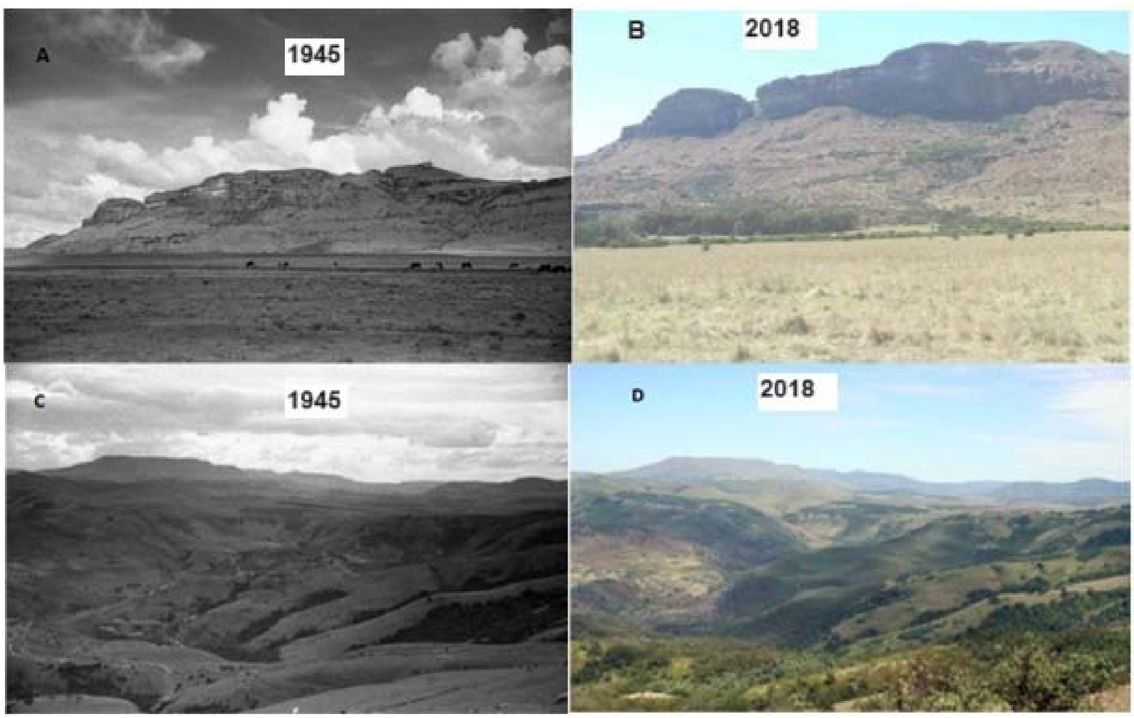

Plate 2. Repeat photography showing *Leucosidea sericea* encroachment in: A (28-01-1945) and B (02-11-2018), Free State province and C (20-11-1945) and D (13-01-2018), KwaZulu Natal Provinces of South Africa. The historical images are freely available online (http://www.cdngiportal.co.za/CDNGIPortal/).

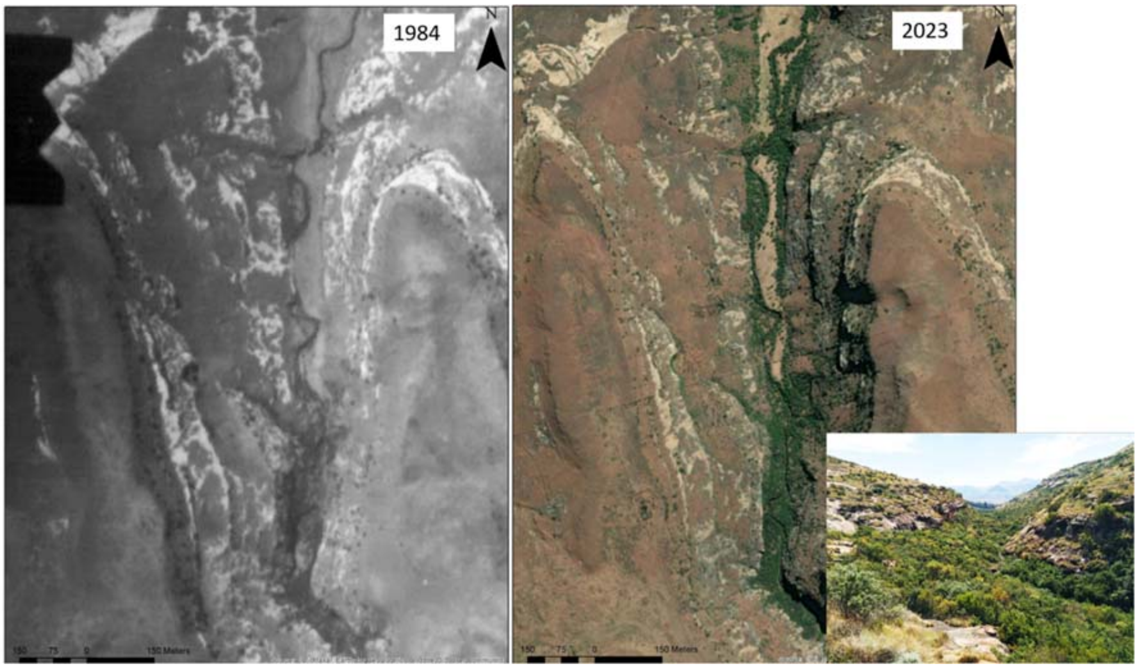

Plate 3. Repeat photography showing *Leucosidea sericea* encroachment near the town of Clarens, Free State Province http://www.cdngiportal.co.za/CDNGIPortal/).

The encroachment seems to be pronounced on 'run-on' areas (i.e. drainage lines) as opposed to 'run-off' areas. Similar patterns have been observed in the field (L. Malekana and S. Steenhuisen, personal observations). In this regard, 'run-off' and 'run-on' dynamics also seem to facilitate encroachment, confirming that *L. sericea* has a high affinity for water. Mogashoa (2017), similarly, found some evidence that *L. sericea* occurred in wetter (but not the wettest) areas in Golden Gate Highlands National Park in the Free State Province. In addition, the same study reported that, at broader scales, annual precipitation was the strongest predictor of *L. sericea* distribution across southern Africa. Isothermality is also correlated with *L. sericea* distribution, and was more influential than precipitation in constraining *L. sericea* distribution in southern African mountains (Gwate et al., 2023).

3.3 Drivers of *Leucosidea sericea* encroachment in southern African mountains

Bush encroachment is ascribed to several drivers, including changes in fire regimes (Westfall et al., 1983; Titshall et al. 2009; de Villiers and O'Connor, 2011), overgrazing, mega-faunal extinctions, climate change, and nutrient fertilisation (Eldridge, et al., 2011). In southern Africa, mega-faunal extinctions occurred predominately in the colonial period (c. 1700–1900), although this process has likely been ongoing since the Late Pleistocene (Rey-Iglesia et al., 2021). The extinction of megafauna in the Late Quaternary had a significant impact on ecosystems, specifically increasing woody vegetation (Rozas-Davila et al., 2016) (in line with findings that suggest mega-herbivore browsing reduces bush encroachment (O'Connor et al., 2014)). For example, Malhi et al. (2016) note that the extinction of herbivorous mega-fauna in arid environments during the Late Pleistocene resulted in a catastrophic increase in fuel load, possibly leading to fire-dominated ecosystems and suppressing woody encroachment. Although mega-faunal extinction also occurred after the Last Glacial Maximum (LGM, 21 000 years BP) (Bakker et al., 2016), charcoal records show a decrease in fires during the LGM (Daniau et al., 2010). However, the vegetation during the LGM was predominantly grassland, and the cooler climate may have contributed to fewer fires than the current warming climate (Mayle et al., 2009; Daniau et al., 2010). For example, in South America during the beginning of LGM period, there was more grassland than forest, probably because of low CO_2 and the destructive activities of mega-fauna (Mayle et al., 2009). Palaeoclimatic studies have also revealed dynamics in *L. sericea* over geological time in response to climate (for example, Stewart and Mitchell, 2018; Finch et al., 2021; Lennox et al., 2022).

Overgrazing is also likely a driver of bush encroachment in both savanna and grassland ecosystems (Shikangalah and Mapani, 2020; Hare et al., 2020; Mogashoa, 2020). In these systems, extensive grazing reduces grass biomass and fuel load, which favours an increase in woody plants (Mogashoa, 2020), leading to a loss of herbaceous cover. At the same time, an increase is browsers could be critical in reducing bush encroachment. For example, in the southern areas of the MD mountains, local goat varieties/breeds, including *Mbuzi* and Xhosa lob-ear ecotypes, have been used to combat the spread of *L. sericea* (https://www.farmersweekly.co.za/animals/cattle/profiting-indigenous-livestock/). In addition, changes in grazing and browsing intensity as well as disturbance in the form of other farming activities may also mediate woody encroachment. For example, the greatest increases in subsistence farming in Lesotho between 1993 and 2013 occurred above 2000 m a.s.l, which corresponds to the high altitudes (2250–2750 m a.s.l) where *L. sericea* communities have densified (Turpie et al., 2021). This suggests that disturbance, including through small scale subsistence farming, may contribute to the expansion of *L. sericea*.

Conversely, depending on soil moisture and precipitation within these systems, heavy grazing can promote grass seed dispersal, with grazers as seed dispersers (Zhang et al., 2017). When this is combined with disturbance and browsing, woody plant development may be impaired resulting in the ecosystem becoming grass dominated. Changes in grazing regimes may influence vegetation structure, and changes in the type of grazing (e.g. shifting from open to controlled grazing) can have similar implications for vegetation structure (Vera, 2000).

In the highveld of South Africa, two categories of plants that encroach into rangelands are recognised: those that increase when the grassland is under-utilised and infrequently burnt, most of which are forest margin species; and those that increase when the grassland is over- or selectively utilised (Schreiner-McGraw et al., 2020). *Leucosidea sericea* increases in both instances (O'Connor et al., 2011). The highest density of *L. sericea* is currently along the mountain grasslands of the Eastern Cape, Free State, and KwaZulu Natal Provinces, and Lesotho. These areas are typified by large commercial farms running primarily livestock (as crop farming is unsuitable in the tough mountain terrain). Until ~1980's, this type of farming predominantly consisted of sheep kept in boundary fences, with occasional large herds of cattle. Between 1980 and 2022, the national sheep flock decreased by 42% (Figure 3), with more pronounced declines in historical sheep farming regions surrounding Lesotho (ttps://vrystaatlandbou.co.za/increase-in-stock-theft-along-lesotho-bordertoename-in-veediefstal-langs-lesothogrens/). Sheep, more so than cattle, can reduce shrub establishment due to the low height to which they graze, and many farmers attribute bush encroachment in their properties to this change in farming practices (i.e., moving away from ranging sheep to combinations of either no grazing, grazing predominantly cattle or penned sheep or cattle). The possibility that the reduction in sheep grazing pressure could be allowing for the increased establishment of *L. sericea* seedlings (previously being eaten by sheep) has, however, not been assessed. Similarly, Turpie et al. (2021) speculated that bush encroachment in the Lesotho highlands was partly driven by overgrazing. In addition, trampling by a large herd of herbivores destroys the seedlings and suppress the growth of the shrub. In this regard, these animals may keep *L. sericea* in check, and future research should consider exploring increased herbivory (especially by specific herbivores, potentially including sheep and megafauna such as Eland) as a management intervention.

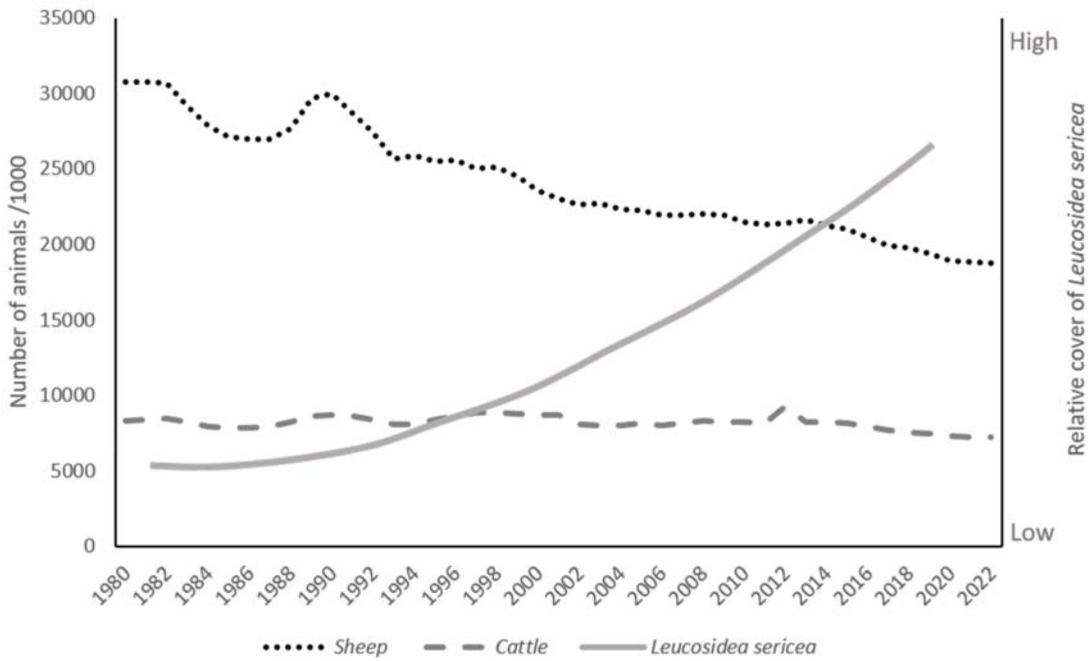

Figure 3. National South African cattle and sheep numbers from 1980 to 2023. (Source: Agriculture, Land Reform and Rural Development (DALRD, 2023). The estimated trend line for *Leucosidea sericea* is inferred from landowner discussion, repeat photographs and authors estimates and not based on any specific data (as none are available).

The southern African Grassland and Savanna Biomes are fire-prone ecosystems, and fire exclusion in these habitats, particularly where rainfall is high, results in the establishment and spread of woody plant species (Mucina et al., 2006). Fire temporarily reduces nutrient and light competition from grasses, and, as a result, woody seedlings can establish, favouring resprouting encroaching species (O'Connor et al., 2014). While burning with a high grass fuel load can kill woody seedlings (O'Connor et al., 2014), lower burning frequencies can allow woody seedlings to establish, potentially leading to bush encroachment (Hare et al., 2020). For example, in north–eastern Namibian savanna, frequent fires have led to the establishment of herbaceous vegetation and reduction in woody cover (Sheuyangea et al., 2005). In contrast, farmers in South Africa have noted that annual winter fires provide only a temporary setback to *L. sericea* growth, as the species survives fires and regrows rapidly after burning (de Villiers and O'Connor, 2011).

Plant-plant interactions can also mediate the success of plants expanding their distributions (and potentially encroaching). For example, preliminary results from an ongoing transplant experiment (Clark et al., unpublished data), revealed that *L. sericea* seedlings survived better when planted without competition in its native range (at ~2200 m a.s.l) under ambient conditions. However, above its current upper elevational limit (~2800 m a.s.l), *L. sericea* seedlings planted within existing vegetation did slightly better than those planted without neighbouring vegetation. These results suggest that facilitative interactions may benefit *L. sericea* as it expands its distribution into higher elevation grasslands (possibly due to relatively frost protection from warmer ambient temperatures in vegetated areas than on bare ground).

The success of invasive alien species in novel environments is often explained by the Enemy Release Hypothesis, which posits that non-native species suffer less from specialist natural enemies (predators, parasites, and herbivores) than native species (Blossey et al., 2011). Indeed, classical weed biological control sometimes rely on the release of a single insect to reduce weed populations (McFadyen, 1998). Currently, there is a global rapid trend of insect extinctions (see Cardoso and Leather, 2019, Cardoso et al,. 2020, and references therein), which will have dire implications, including increased spread of weedy species (van der Sluijs, 2020). Therefore, early signs of spreading weed species should not be easily dismissed.

In the 1980's, Louw (1988) examined the arboreal Coleoptera associated with *L. sericea* at Golden Gate Highlands National Park (Free State Province, South Africa) for 13 consecutive months at five sites. A high diversity of insects was associated with the species, with 117 species of Coleoptera representing 35 families, and multiple ecological strategies: phytophages (47 species), predators (44 species), scavengers (16 species), and 'tourists' (10 species). The study has not been replicated to determine current insect density and diversity, however, personal in-field observations (G. Martin, personal observation) of species on *L. sericea* growing in the landscape suggest a lower insect diversity than recoded in the 1980's.

Increasing atmospheric CO_2 concentrations and the associated patterns of climate change are regarded as the most important factors driving woody encroachment in southern Africa (Bond and Midgley, 2000). For example, elevated atmospheric CO_2 has been linked to woody thickening and woody encroachment in southern Africa (Wigley et al., 2009; O'Connor et al., 2014; Stevens et al., 2016; Shikangalah et al., 2020). The connection between enriched atmospheric CO_2 and its benefits to plants with a C_3 photosynthetic pathway – including most woody plants – is now considered a major driver of encroachment (Venter et al., 2018). Consequently, ecosystems are forecast to become more dominated by C_3 plants (Bentley and O'Connor, 2018). It should be noted that during glacial periods (i.e., LGM, when atmospheric CO_2 was lower), ecosystems were dominated by C_4 species (Belayneh et al., 2017). This is probably because C_4 species have lower nitrogen and moisture requirements than the C_3 species (Nippert et al., 2007). C_3 species have been found to be more responsive to CO_2 concentrations than C_4 species (Wigley et al., 2009). For example, the response of C_3 plants to rising CO_2 levels is expected to result in range expansion (Bond and Midgley, 2000). Nitrogen fertilisation also has similar effects on woody encroachment (Pillay et al., 2021). However, with respect to *L. sericea*, Gwate et al. (2023) reported habitat contraction under climate change scenarios encapsulated by representative concentration pathways (RCPs) 4.5 and 8.5. In addition, Lebese (2021) reported that experimentally increasing temperature or CO_2 concentration did not affect *L. sericea* growth. Preliminary results from an ongoing experiment (Clark et al., unpublished data) to test the mechanisms underlying the success of range expanding plants in the MD mountains indicate that survival ratio (0.57) of *L. sericea* seedlings planted in competition was higher than for those planted without competition (0.33) under climate warming of c. 2°C. This confirms that facilitative interactions, potentially more than climate, maybe be important in mediating *L. sericea* survival beyond its native range in the MD region. Changes in rainfall seasonality and reliability, caused by climate change, could encourage shifts in vegetation structure. For example, winter rainfall is likely to favour the expansion of woody plants, with summer rainfall favouring grasses, while an increase in temperature is forecast to favour woody species over grasses (Bond and Midgley, 2000; Browning et al., 2008; O'Connor et al, 2014). An increase in rainfall could lead to increased soil moisture in environments where grasses and deeper-rooted woody species compete for moisture, resulting in woody species outcompeting grasses (Turpie et al., 2019).

In summary, while consensus is emerging that *L. sericea* is encroaching, mechanisms underlying this encroachment need to be explored further. For example, it is not well understood if the current trajectory will continue under future climate change. Hence, more rigorous modelling and experimental studies will be required to better understand potential range shifts and the biology of the species. Indeed, the lack of published experimental studies suggests that there may be considerable value to conducting even basic experimental studies on this species. Models that combine several interacting variables including climate, land use, fire, and dispersal barriers will be most useful to better understand the biology, impact and distribution of the species.

3.4 Potential impacts and management of *Leucosidea sericea*

Although field observations (and some limited data) suggest that *L. sericea* is encroaching in the MD, little is known about its impacts on, for example, montane biodiversity (Turpie et al., 2019). Ongoing research in the Clarens area of the eastern Free State Province has shown that increased shade, reduced soil temperature, and change in soil edaphic factors created by woody encroachment (including *L. sericea*) has resulted changes in the grassland plant communities (L. Malekana et al., unpublished data). This in turn will have direct impacts on grazing capacity and stocking units. Southern African montane grasslands support exceptionally high floral and faunal diversity, and an increase in woody cover may dramatically reduce such diversity (Koch et al., 2015). As an example, a steady loss of montane grassland in the Soutpansberg has been ascribed to bush encroachment, with negative impacts on endemic biodiversity (Hahn, 2017). Similarly, higher elevation montane grassland in the Great Winterberg–Amatholes (Eastern Cape, South Africa) is readily encroached by woody fynbos in the absence of fire (Clark et al., 2014). On the other hand, lower elevation scarp slopes have become visibly encroached by woody thicket species over the past 40 years, with a general increase in woodiness also evident on the drier, northern side of the Great Winterberg mountains (L. King, pers. comm.). Such bush encroachment can potentially limit habitat availability for local endemics, many of which are highly-localised grassland species (Clark et al., 2014). Woody encroachment in the eastern Free State Province is also changing the grassland ecosystem and associated biodiversity (Adams et al., 2017). For example, increased bush cover provides protection from predators for many rodents and changes the availability of forage sources. A biome that was previously food-scarce during long harsh winters is increasingly becoming food-rich, allowing for the proliferation of frugivores and rodents. Increasing rodent numbers and frugivores bird species may create some ‘winners’ and ‘losers’ within the mammal as well plant communities. Larger mammal species have also started to change distributions moving into the now more savanna-like grassland environments. Increased abundance in certain animal species including nyala, bushbuck, waterbuck, bush pig, and warthogs into the grassland have already been noticed (see recent iNaturalist records; https://www.inaturalist.org/). In addition, bush encroachment more generally may reduce herbaceous plant biomass and density (Siraj and Abdella, 2018), but the link between encroachment and ecosystem change is not universal (Eldridge et al., 2011).

Woody encroachment can lead to the abandonment of montane grassland by local communities (van den Bergh et al., 2018), chiefly due to the loss of palatable herbaceous and grass species layers for livestock (Lesoli et al., 2013; O'Connor et al., 2014). However, there is no data yet on how *L. sericea* encroachment affects rangeland productivity – but it is perceived that it degrades the system (Ndamane et al. 2023). In contrast to negative impacts on agricultural production, some encroaching species (including *L. sericea*) may also have some benefits to the local economy since they provide firewood and shelter, especially in rural areas (Ngorima and Shackleton, 2019).

Woody plant encroachment alters the exchange of mass and energy between the land surface and the atmosphere. For example, encroachment may increase ambient temperature by reducing canopy albedo (Wang et al., 2021). However, the canopy of some invasive plants may also lower understorey temperature by reducing light penetration through the canopy (Chikowore et al., 2021b). The replacement of grasslands by woody cover could also result in an increase in groundwater abstraction owing to the deeper root systems of trees and shrubs compared to grass species (Le Maitre et al., 1999), resulting in an altered moisture regime including, diminished groundwater discharge (Acharya et al. 2018). The relatively higher water-use of encroaching woody vegetation in South Africa has already been demonstrated (Le Maitre et al., 2015; Dzikiti et al., 2023), but water use of *L. sericea* has not been described adequately, and we found only one study (Gray et al., 2021). As a result, changes in the structure and physiology of dominant vegetation can strongly affect hydrological processes and, negatively impact biodiversity (Le Maitre et al., 2015). Moreover, with an increase in woody cover, the amount of rainfall reaching the ground surface is reduced owing to greater interception (Villegas et al., 2015). Evapotranspiration observations from the northern Drakensberg showed that over time, as woody encroachment increased, runoff response increased compared to natural grassland (Gray, 2021).

Owing to the emerging consensus among grassland ecologists that *L. sericea* is encroaching, management interventions to control its spread in the Free State Province of South Africa have been implemented by the Working for Water programme (Table 1). This is a public works programme that seeks to, simultaneously reduce poverty and control range expanding plants to restore affected ecosystems (Turpie et al., 2008). The management approach by the Working for Water programme revolves around clear felling and application of herbicides. For example, < 5% of the projected 2713.73 ha of *L. sericea* encroachment area at twelve sites in the eastern Free State province of South Africa was treated at a cost of ZAR654 277.75 (~US$34 435.00). In additional control efforts, farmers have tried using fire and herbicides to manage *L. sericea* but have reported that regrowth after fires was massive (de Villiers and O'Connor, 2011) and chemicals were prohibitively expensive and could result in negative externalities. Thinning could also be an option to reduce the canopy of *L. sericea* and promote undergrowth vegetation to enhance multi-benefits of the plant (Dwyer et al, 2010).

Table 1. Extent of *Leucosidea sericea* occurrence and area treated in the eastern Free State province of South Africa (Free State Department of Forestry, Fisheries and the Environment) in twelve intervention actions (2015–2021).

Area cleared (ha)	Total Projected potential distribution (ha)	Initial Total Density (trees ha^{-1})	Total Cost (ZAR)	First Date Treated	Last Date Treated
20.53	370	85	94 605	2015/10/07	2017/10/27
4.89	50	80	12 852	2015/11/16	2015/11/20
19.66	584	80	135 927	2015/11/30	2020/12/09
14.33	295	75	67 348	2016/02/05	2020/10/08
16.65	318	81	70 878	2015/10/07	2020/10/08
9.11	212	82	55 490	2015/10/07	2021/02/10
6.25	96	80	23 532	2017/03/13	2021/02/11
11.81	181	75	44 851	2017/03/13	2021/02/11

	186	85	45 471	2017/03/13	2020/11/30
9.43					
	190	95	47 697	2017/12/04	2021/03/31
8.05					
	186	95	47 411	2017/12/04	2021/03/31
6.67					
4.65	45	95	8 217	2017/12/04	2018/01/25
132.03	**2714**		**654278**		

Finally, literature suggests that the general impacts of bush encroachment are well understood. However, there is a dearth of studies on the impacts of *L. sericea* encroachment on various receptors. We found one article on community perception on the impacts (Ndamane et al., 2023) and one study that highlighted water use dynamics of *L. sericea* (Gray et al., 2021). Published studies on the impacts of biodiversity and management of *L. sericea* were conspicuously absent and this requires urgent attention considering the concerns about this species. Requisite legislation and policy are required for the management of indigenous range expanding plants such as *L. sericea*.

6. Conclusion

Both global factors, like CO_2 fertilisation, and local factors, such as disturbance and herbivory, potentially interact to shape the process of bush encroachment. As a result, to improve our understanding of bush encroachment, multi-disciplinary and multi-partnership approaches should be adopted in evaluating the process and multi-factorial experiments may be necessary to tease out the interactions among the causal factors of bush encroachment. Once these factors have been determined, management options to sustainably utilise rangelands can be tailored accordingly. Unfortunately, research into the specifics of the impacts and the magnitude is only now in progress. Data is currently limited to *ad hoc* investigations, but ecosystem functioning, and the associated ecosystem services, are likely being impacted, potentially with important effects on the communities relying on this biome for resources. Rigorous and geographically comprehensive quantitative studies are required to better describe the extent and rate of *L. sericea*'s expansion, and the species fine- and broad-scale ecological impacts. Although *L. sericea* may be regarded as a troublesome encroacher species, it remains a southern African endemic with local social-ecological value. As a result, optimal management of *L. sericea* must balance needs. However, future research on the influence of fire on *L. sericea* distribution, water use, insect herbivory, and changing farming practices should be a priority to guide the management of *L. sericea.*

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