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RESEARCH ARTICLE

Seed banks and post-fire recovery of invasive alien *Metrosideros excelsa* in South Africa: Implications for control

Tineke Kraaij[1] | **Sjirk Geerts**[2] | **Nicole Malan**[1,3]

[1]Natural Resource Science and Management Cluster, Faculty of Science, Nelson Mandela University, George, South Africa

[2]Department of Conservation and Marine Sciences, Cape Peninsula University of Technology, Cape Town, South Africa

[3]South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa

Correspondence
Tineke Kraaij, Natural Resource Science and Management Cluster, Faculty of Science, Nelson Mandela University, Private Bag X6531, George 6530, South Africa.
Email: tineke.kraaij@mandela.ac.za

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South African Department of Forestry, Fisheries, and the Environment; Cape Peninsula University of Technology; Nelson Mandela University; South African National Biodiversity Institute

Abstract

The New Zealand bottlebrush, *Metrosideros excelsa* (Myrtaceae), was introduced into South Africa in the 1940s as an ornamental plant and subsequently naturalized in coastal parts of the Cape Floristic Region. Knowledge of *M. excelsa*'s propagule pressure and response to fire in South Africa can inform evaluation of the species' invasion potential and management. We assessed *M. excelsa*'s canopy and soil seed banks in burnt and unburnt stands; and post-fire regeneration via reseeding and resprouting in relation to fire severity and tree size. Soil seed banks were assessed using an emergence technique, but no seedlings emerged from soil collected under burnt or unburnt plants suggesting that the species does not maintain a viable soil-stored seed bank or germination triggers were not met (though unlikely). The annual seed crop in the canopies of unburnt trees was approximately 0.5–23 million seeds per tree. Viability, assessed through tetrazolium stain testing, of canopy-borne seeds on unburnt trees was 18%, whereas a canopy fire, ranging in severity from low to extreme, killed all canopy-borne seeds. Fifteen months post-fire, the seedling to pre-fire (live) tree ratio was 0.01, whereas 43% of burnt trees survived via basal resprouting. Fire severity had a non-linear effect on tree survival (survival was highest after medium and high fire severity and lowest after low and extreme fire severity), while larger trees were more likely to survive fire. These results suggest that even low-severity (safe) burning may be a useful control measure as it kills canopy-borne seeds and causes substantial mortality, particularly of smaller trees. An opportunistic evaluation of an uncontrolled (no comparison with untreated individuals) foliar herbicide application to post-fire resprouting individuals also showed considerable (91%) mortality. However, rigorous herbicide trials (also with herbicide in conjunction with burning) are required to inform the management of *M. excelsa*.

KEYWORDS
fire severity, herbicide, post-fire regeneration, propagule pressure, viable seed crop

INTRODUCTION

Invasive alien species significantly influence global biodiversity and cause substantial socio-economic losses (Castro-Díez et al., 2019; Diagne et al., 2021; Pyšek, Hulme, et al., 2020). Factors influencing the success of invasive alien plant (IAP) species are complex and interactive. These

comprise the traits of a species and properties of an ecosystem that make it vulnerable or resistant to invasion, e.g., the disturbance regimes and introduction history relating to propagule pressure and residence time (Catford et al., 2009; Moodley et al., 2013; Pyšek, Bacher, et al., 2020). Understanding an alien species' ecology, such as its seed ecology and response to disturbances, is thus pertinent in invasion science to inform a species' invasive potential and suitable management responses (Eschtruth & Battles, 2009).

Propagule pressure refers to the rate and volume at which regenerative propagules, like seeds or ramets, are released into and persist in environments (Lockwood et al., 2005), which is directly related to the likelihood of an alien species becoming invasive (Colautti et al., 2006). The quantification of species' viable seed banks is thus vital for determining invasive potential and eradication feasibility (Eschtruth & Battles, 2009; Goets et al., 2018).

Disturbance generally predicts invasion at a localized scale (Hobbs & Huenneke, 1992; Richardson et al., 2020). Disturbance facilitates invasion by eliminating competition from native species, releasing resources and stimulating germination (Goets et al., 2018; Hierro et al., 2006). A globally common and important disturbance is fire, which may interact with alien plant invasion. Fire creates opportunities for plant recruitment (Pausas & Keeley, 2009) but native fire regimes may also be altered by IAPs, which can facilitate further invasion (Brooks et al., 2004; Hobbs & Huenneke, 1992). However, the traits of a species will determine how it reacts to fire (Geerts et al., 2013; Hobbs & Huenneke, 1992).

Here we explored the propagule pressure and response to fire of *Metrosideros excelsa* Soland *ex* Gaertn., the New Zealand bottlebrush or New Zealand Christmas tree (Myrtaceae family), in its invaded range in South Africa. *Metrosideros excelsa* is primarily a coastal species native to northern New Zealand (Bergin & Hosking, 2006) but was introduced to southern New Zealand, Australia, the Caribbean, North America, Europe and South Africa (Dawson, 2014; Malan, 2023). The species was introduced into South Africa as an ornamental plant in the 1940s (Bylsma et al., 2014; Richardson & Rejmánek, 1999; Sreekantan et al., 2001) when it was considered a safer hedging alternative to the aggressive invader, *Leptospermum laevigatum* (Gaertn.) F. Muell, another member of the Myrtaceae family (Richardson & Rejmánek, 1999, 2011). *Metrosideros excelsa* naturalized in the early 1980s in the coastal town of Betty's Bay in the Cape Floristic Region, particularly at sites with seasonally moist, peat-like soils (Richardson & Rejmánek, 1999). A recent, wider-ranging study showed that the species has a preference for fynbos-dominated areas and dune habitat types at low altitude, on flat slopes and sandy and seasonally wet substrates (Malan, 2023). A species distribution model predicted *M. excelsa* to be bioclimatically suited to the tropics, sub-tropics, coastal Mediterranean and temperate regions of the globe, including most of the South African coastline, suggesting potential for expansion beyond its current range (Malan, 2023). However, the predicted suitable area in South Africa is likely to be more limited when considering suitability for natural regeneration as opposed to cultivated specimens.

Knowledge of the ecology of *M. excelsa* is largely based on studies in the native range (detailed in Methods), with limited information available on its ecology in its introduced range. Like invasive *Melaleuca* species (also from the Myrtaceae family), *M. excelsa*, in its native range, produces copious quantities of wind-dispersed seeds that need wet habitats to germinate (Hickley et al., 2017). At Betty's Bay in South Africa, it has been shown that seedling establishment of *M. excelsa* was equally dependent on propagule pressure and on soil moisture (Rejmánek et al., 2013), with dense seedling

stands that have been recorded at distances of up to 80 m from stands of adult trees (Richardson & Rejmánek, 1999). In its native range, *M. excelsa* is considered to have transient seed banks (Schmidt-Adam et al., 2002), but no prior study investigated whether the species maintains short-lived, soil-stored seed banks in its introduced range, or whether its seeds can survive fire.

Presently in South Africa, *M. excelsa* seems invasive in the Fynbos Biome only (Malan, 2023), a fire-prone ecosystem where other successful woody invaders are adapted to the native fire regimes through possessing traits that enable proliferation after fire via reseeding (e.g., *Pinus* and *Hakea* species), resprouting (e.g., *Eucalyptus* species), or both (e.g., *Acacia* species) (van Wilgen, 2009). Although in its native range, *M. excelsa*'s establishment from seed is linked to stochastic disturbance events, where it colonizes early volcanic substrates, landslides and burnt areas, the species is also deemed fire sensitive as low-intensity fires can kill mature trees and seeds and resprouting has rarely been witnessed as a means of post-fire survival (Atkinson, 2004; Bylsma et al., 2014; Clarkson, 1990). It is thus pertinent to comprehend the seed ecology and regeneration or persistence strategies in relation to fire of *M. excelsa* in its introduced range to gain further insights into the species' invasive capabilities and to develop suitable management approaches.

Despite uncoordinated attempts to manage the spread of *M. excelsa* in South Africa since the 1980s (Henderson, 1998; Richardson & Rejmánek, 1999), herbicides have not been legally registered (Harris, 2002) and a coherent management strategy does not exist for the species (Higgins et al., 1999). The largest known invasive population of *M. excelsa* in South Africa, in Betty's Bay, burnt down in January 2019 in a wildfire, which presented an opportunity to study the species' response to fire and thus to assess burning as a potential means of control. Additionally, residents opportunistically applied herbicide to some of the *M. excelsa* trees resprouting after the 2019 fire which allowed an ad hoc evaluation of the effectiveness of this herbicide treatment.

The aims of this study were therefore to (i) quantify the propagule pressure of *M. excelsa* in terms of viable canopy and soil seed banks in unburnt and burnt stands, (ii) assess post-fire regeneration success of *M. excelsa* by determining post-fire recruitment from seed and post-fire survival through resprouting of established individuals in relation to fire severity and tree size, and (iii) take the opportunity of an uncontrolled foliar application of herbicide to evaluate the impact on post-fire resprouting individuals.

METHODS

Study species

Metrosideros excelsa is a tree up to 25 m tall and 50 cm or more in diameter at breast height, forming a significant element of northern New Zeland's coastal vegetation (Bylsma et al., 2014; Clarkson & Clarkson, 1994). Its reproductive strategy in its native range has been described as 'wasteful but sufficient' (Schmidt-Adam et al., 2002) as a single tree can produce up to 40,000 flowers in a mast fruiting season and although only 10% of ovules develop into viable seeds, the overall seed production per tree remains high (Bergin & Hosking, 2006; Bylsma et al., 2014). The breeding system is intermediate between facultative selfing and facultative outcrossing and the flowers are hermaphroditic (Bylsma et al., 2014). The species is associated with a diversity of pollinators, including birds, bees, honeybees, geckos and bats (Bylsma et al., 2014). When viable seeds were harvested and

immediately planted, the germination rate was 99%, while 58% remained viable for 6 months at room temperature and no seeds were viable after 1 year (Schmidt-Adam, 1999; Schmidt-Adam et al., 2002). Seeds are 3.0–3.2 mm in length by 0.2–0.42 mm in width and weigh 0.1–0.15 mg (Schmidt-Adam et al., 2002). The small seeds are readily dispersed by wind, ensuring long-distance dispersal even with light winds of 5–19 km/h (Bylsma et al., 2014; Schmidt-Adam et al., 2002; Wright et al., 2000). Dispersed seeds are extremely hardy, surviving temperatures of up to 230°C for 6 h and they can be submerged in salt water for up to a month (Schmidt-Adam et al., 2002; Wright et al., 2000). However, the seed bank is deemed transient as seeds lack endosperm tissue and have a thin seed coat, rendering them very vulnerable to desiccation (Bergin & Hosking, 2006; Bylsma et al., 2014). After dispersal, seeds persist for a few months only and must germinate soon after seed fall in summer or early autumn (Atkinson, 2004; Schmidt-Adam et al., 2002). Successful establishment of *M. excelsa* thus requires synchrony between seed set, dispersal and conditions (i.e. high light and water availability, without dense leaf litter) suitable for germination (Britton-Simmons & Abbott, 2008; Bylsma et al., 2014).

Although the natural incidence of fire is low in the species' native range (Perry et al., 2014; Teixeira et al., 2020), archaeological evidence points to regular human-induced fires during the Māori occupation of northern New Zealand (Atkinson, 2004; Ogden et al., 1998). *Metrosideros excelsa* rarely spreads in the absence of disturbance and even small, localized disturbances, such as rockfalls or landslides, can facilitate the establishment of small, localized populations (Atkinson, 2004; Bylsma et al., 2014). The species thus typically occurs as even-aged stands that are shade-intolerant (Atkinson, 2004). Given the right conditions, stands of *M. excelsa* can maintain a continuous canopy, thereby retarding succession for at least 100 years, while individual trees can live for 300 years or more (Atkinson, 2004). Re-establishment can also occur via vegetative regeneration, through adventitious roots on fallen stumps (Bergin & Hosking, 2006). Although disturbance may allow *M. excelsa* to establish, the species is deemed to be fire-sensitive in New Zealand, with post-fire recruitment from seeds being dependent on seed dispersal from unburnt mature trees in the immediate vicinity (Atkinson, 2004; Bergin & Hosking, 2006; Bylsma et al., 2014).

Conversely, *M. excelsa* has traits suggestive of adaptation to fire, such as, woody capsules presumably protecting the seeds from heat and dehydration, production of large quantities of dead leaf litter and thus fuel, oil glands in the leaves, thick flaky bark and dense wood with low moisture content, all promoting flammability (Bylsma et al., 2014; Perry et al., 2014; Solangaarachchi & Gould, 2001). Trees readily produce adventitious roots and although *M. excelsa* can resprout from epicormic buds on the lower part of the trunk and on branches under diverse circumstances (e.g. after damage from volcanic activity; Clarkson & Clarkson, 1994), resprouting as a means of post-fire survival is rare (Bergin & Hosking, 2006; Bylsma et al., 2014). Clarkson and Clarkson (1994) found limited evidence that stem size affected *M. excelsa* resprouting success after volcanic activity on White Island, New Zealand and observed high mortality of the resprouts. Generally, individuals of *M. excelsa* are often multi-stemmed, as trees established in open sites from seed commonly develop multiple stems at an early stage, rather than the trait being suggestive of post-fire resprouting (Atkinson, 2004). The fragmented distribution of *M. excelsa* populations in its native range suggests that too high an intensity or frequency of disturbance kills individual trees and prevents re-establishment (Bergin & Hosking, 2006; Bylsma et al., 2014).

Study area

Betty's Bay (34.21094° S 18.55347° E), located in the Overberg district, was chosen as the study area due to it being the only known place in South Africa with a substantial invasive population of *M. excelsa* (Malan, 2023). The town is situated on a narrow coastal plain at the foot of the Kogelberg Mountains (reaching 816 m above sea level), which form part of the Table Mountain Group (Rebelo et al., 2006; Winter, 2006). Nutrient-poor, sandy dunes predominate, formed from marine and aeolian sediments (Mitchell et al., 1984; Winter, 2006). A Mediterranean climate prevails with hot, dry summers and wet winters (Peel et al., 2007; Rebelo et al., 2006). The mean annual temperature is mild (15°C) and the area has the highest rainfall (mean annual precipitation of 1330 mm) in the Cape (Rebelo et al., 2006). Coastal fog and regular orographic rain ensure moist conditions (Rebelo et al., 2006; Winter, 2006). Streams from the mountains are impounded by dunes, forming seeps, a shallow underground water table and acidic black-water systems. Within these areas, vegetation that is diagnostic of moist areas, such as members of the Bruniaceae family occurs (Rebelo et al., 2006). Rain is typically preceded by cold fronts associated with strong south-westerly winds (Kruger et al., 2010; Tinley, 1985). In summer, strong and persistent south-easterly winds have a drying effect on the vegetation (Kruger et al., 2010; Tinley, 1985). Fires in fynbos most commonly occur during the summer months, with fire return intervals ranging from five to 22 years and these generally are intense and severe crown fires (Kraaij & van Wilgen, 2014; van Wilgen et al., 2010).

The area of Betty's Bay is a wildland-urban interface, with the town occurring on the edge of the Kogelberg Biosphere Reserve. The Kogelberg is a hotspot of plant diversity and endemism within the hyperdiverse Cape Floristic region (Cowling et al., 1996), however, the region is increasingly threatened by the spread of IAPs, urbanization and frequent fires (Richardson & Rejmánek, 1999). The native vegetation comprises various types of fynbos, including Cape lowland freshwater wetlands, Kogelberg sandstone fynbos, Hangklip sand fynbos, Western coastal shale band vegetation and Overberg dune strandveld. These fynbos types predominantly support restiod and ericoid species (<5 m tall) (Mitchell et al., 1984; Rebelo et al., 2006). Cape seashore vegetation, comprising herbaceous and shrub-like plants, occurs on the dunes (Mucina et al., 2006). The small growth forms are easily suppressed by taller woody species (Cowling et al., 1996).

Metrosideros excelsa has invaded moist areas in Betty's Bay (Malan, 2023), where it threatens the persistence of native endemic and rare species (Rebelo et al., 2006). Fires in the adjacent Kogelberg Biosphere Reserve recur on average every 16 years (van Wilgen et al., 2010) but burn less frequently in the town itself, where the only recent fires were in 1970 (Spriggs, 1995) and 2019 (Chambers, 2019). The 2019 fire was of human origin, burnt a total of 13 000 ha and occurred in January during the peak of the dry summer period with strong north-westerly winds of up to 100 km/h (Chambers, 2019). The only known large (3.3 ha) and dense stand of *M. excelsa* occurs towards the eastern edge of the town and was burnt in this surface-to-canopy fire (Figure 1a,b). A few unburnt trees of *M. excelsa* occur approx. 2.5 km west of the burnt stand, whereas several unburnt planted hedges comprising numerous mature individuals occur towards the western edge of the town, approx. 7 km from the burnt stand.

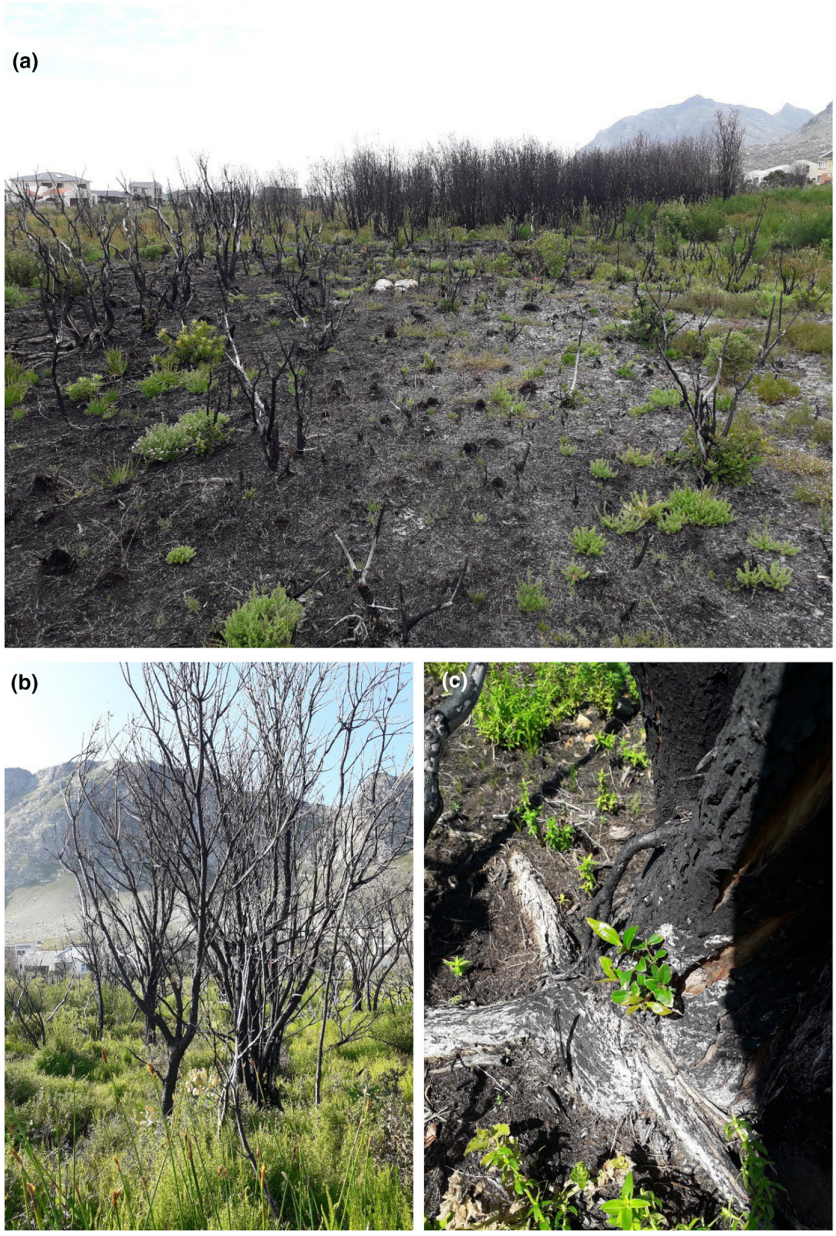

FIGURE 1 *Metrosideros excelsa* post-fire in South African fynbos at the study site at Betty's Bay. (a) The post-fire landscape. (b) Burnt adult *M. excelsa* trees. (c) A burnt individual exhibiting post-fire basal resprouting.

Soil seed bank sampling

The densities and viability of soil seed banks were determined in transects located within unburnt planted hedges and in the burnt stand of *M. excelsa* trees at Betty's Bay. The aim was to enumerate the previous (2018) season's soil seed bank in unburnt areas and determine whether any soil-stored seeds survived the January 2019 fire. Although this was deemed unlikely given what is known about the species' seed ecology in its native range, it remained to be verified for the introduced range. Seeds are usually released during March and April each year in New Zealand (Bergin & Hosking, 2006); we therefore sampled soil at the end of March 2019, prior to the extensive opening of seed capsules of the 2019 season. Seed banks were sampled from underneath a range of tree densities and sizes. In both the unburnt hedges and burnt stand, 10 transects each of 10×5 m were

located (coordinates recorded with a GPS) and spaced at least 5 m apart. In each transect, the soil was sampled at three locations, spaced 3 m apart along the longitudinal central axis of the transect. This provided 30 soil samples each from the unburnt hedges and burnt stands. The leaf litter layer was scraped away to avoid substantive sampling of seeds potentially released during the 2019 season (as sampling was aimed at the 2018 seed crop contained in the soil). For each sample, the soil was collected over a rectangular surface area of 30 × 15 cm and to a depth of 5 cm, as this zone contains most seeds (Bakker et al., 1996; Goets et al., 2018).

The small size of the seeds rendered sieving seeds or manual extraction from the soil futile (Bakker et al., 1996) and an emergence technique (Dreber, 2011; Wright & Clarke, 2009) was thus used to estimate the number of viable seeds contained in the soil. The soil samples were placed in brown paper bags (to avoid moulding) when collected and thereafter stored in open polyethylene bags to prevent the paper bags from tearing (Wright & Clarke, 2009). They were stored for 3 weeks in a cool laboratory (18°C ambient temperature) on the George Campus of Nelson Mandela University after which the emergence trial commenced. Aluminium trays (36 × 26 × 6.5 cm) were filled with potting soil to a depth of 3 cm and the soil samples were spread evenly on top of the potting soil (Bakker et al., 1996). The unburnt and burnt soil sample trays were placed in a randomized order within a baboon-proof enclosure on the same campus. The trays were exposed to open air and full sun (Wright & Clarke, 2009). The soil samples were watered daily to maintain soil saturation and to prevent seed desiccation (Dreber, 2011; Wright & Clarke, 2009). If rain was forecast, the samples were not watered shortly before, during and shortly after rainfall events to prevent flooding of the soil. These conditions are deemed suitable to promote the seedling emergence of this species (Bakker et al., 1996). The emergence of seedlings was monitored daily for 3 months (Pierce & Cowling, 1991; Wright & Clarke, 2009) as seedling emergence was expected to cease beyond this period (Dreber, 2011).

Canopy seed bank sampling

Seeds in the canopies of unburnt trees of various sizes were sampled from the same unburnt planted hedges where soil sampling was done to estimate the annual seed crop of *M. excelsa*. Seed sampling was done towards the end of April 2019 as most mature trees had fully developed seed capsule clusters by then (cf. Bergin & Hosking, 2006; Bylsma et al., 2014). A total of 54 mature trees within the unburnt hedges were surveyed for the number of capsule clusters borne and their height was estimated to the nearest meter (as an easily measured proxy for tree size). Complete counts of capsule clusters were only feasible for small trees. For larger trees, for which complete counts were not feasible, the number of capsule clusters borne was estimated by progressively dividing the tree into smaller units until a total count of capsule clusters could be done for that unit. In these cases, the number of main stems was counted, followed by the number of branches per stem and the number of side branches per branch. Subsequently, a simple multiplication was done to estimate the total number of capsule clusters borne by a tree (Enright et al., 2007; Schmidt-Adam, 1999).

To obtain an estimate of the mean number of seeds contained in a capsule, we randomly selected 50 unburnt trees of varying heights and collected one capsule cluster from each. Capsule clusters were only collected to a maximum height of 2 m. The capsules were stored at room temperature for 3 weeks in brown paper bags in the same laboratory as the soil samples. To count the total number of seeds borne per tree, only the

capsule clusters from unburnt trees were used. The total number of capsules in each capsule cluster was counted to estimate the mean number of capsules per cluster. Thereafter, the mean number of seeds per capsule was estimated by selecting one capsule from a cluster. A subsample of seeds was counted and weighed per capsule, after which all the seeds in the capsule were weighed. We then calculated the mean number of seeds per capsule cluster to ultimately obtain a crude estimate of the total number of seeds borne per tree (Enright et al., 2007; Goubitz et al., 2004).

To assess the seed viability of seeds borne by unburnt trees, the seeds extracted from the capsules of unburnt trees were used. To assess the seed viability of seeds borne by burnt trees, we collected five capsule clusters each from 10 burnt trees of varying heights. These were the only trees within the burnt stand that bore fully developed capsules which persisted through the fire and that visibly experienced low crown fire severity (see details of fire severity ratings below) compared to the other trees of which the capsules presumably were consumed by the fire. The seeds extracted from the capsules of the burnt and unburnt trees were stored in separate brown bags in a refrigerator at 4°C to ensure seed longevity (Schmidt-Adam et al., 2002). We also kept seeds from dry and green capsules of unburnt trees apart as uncertainty existed about the maturity of seeds from visibly dry versus green capsules. Seed viability was determined using a tetrazolium stain test (Peters, 2000). Three hundred seeds randomly selected from each of the dry, green and burnt capsules were divided into 15 petri dishes containing 20 seeds each and the number of stained seeds counted. The petri dish batches of 20 seeds each comprised the unit of replication, i.e., there were 15 replicates for each of the seeds from dry, green and burnt capsules. The seeds were soaked in filtered water for 24 h. They were then stained in a 1% aqueous solution of 2, 3 and 5 triphenyl-tetrazolium chloride for 72 h at 37°C in a dark oven (Peters, 2000). The seeds were thereafter inspected for staining under a dissecting microscope and inspection was repeated after 48 h of exposure to natural light inside the laboratory to determine whether additional staining had occurred. Seeds that stained red were considered viable (Pierce & Cowling, 1991; Schmidt-Adam et al., 2002). This enabled seed viability to be estimated and subsequent estimation of the size of viable seed crops produced annually by trees of different sizes.

Response to fire surveys

Post-fire regeneration of *M. excelsa* was assessed in the burnt stand during March 2020, i.e. 15 months after the 2019 fire to ensure adequate time had elapsed for regeneration via resprouting and for seed germination to have occurred (Enloe et al., 2018; Kraaij et al., 2013; Lloret & López-Soria, 1993). Transects were positioned to include various densities and sizes of pre-fire *M. excelsa* trees that appeared to have experienced various levels of fire severity (Catry et al., 2010; Morrison, 2002). Burnt individuals of *M. excelsa* were identified based on canopy architecture, bark texture and remains of leaves or capsule clusters (Bylsma et al., 2014; Marais et al., 2014; Teixeira et al., 2020).

In 11 transects of 50 × 2 m, regeneration from seed was recorded by counting the number of seedlings in relation to the number of pre-fire (burnt) individuals (basal diameter >1 cm) of *M. excelsa*. Various multi-stemmed individuals were often growing close together, in which case they were considered distinct individuals when stems were not joined (Tomback et al., 1993). In these same transects, the survival of each pre-fire *M. excelsa* individual ($n = 699$) was assessed in relation to its pre-fire dimensions

and the fire severity experienced. It was presumed from the stature of the burnt trees, the texture of the burnt wood and the occasional presence of burnt leaves that these individuals were alive before the fire. Stem diameter at ground level (DGL) was measured at the widest point as a measure of pre-fire plant size (Lloret & López-Soria, 1993; Marais et al., 2014). The fire severity experienced by each individual was furthermore scored by visually assessing the damage to the bark and wood at the base of the stem as follows: 1 = low (bark black, but intact), 2 = medium (considerable fire damage to bark), 3 = high (bark burnt away and wood moderately damaged), or 4 = extreme (wood severely damaged, charcoaled or burnt away) (Appendix S1; Chafer et al., 2004; Giddey et al., 2021; Strydom et al., 2020). Fire severity in the canopy of trees was assessed similarly but the scores were correlated with fire severity at the base of stems and thus not used in analyses. Individuals were considered to have survived if they exhibited basal lignotuberous resprouting (from the base of the main stem) or aerial epicormic resprouting (higher up along the main stem or from branches in the canopy) (Clarke et al., 2013) and were assumed dead when no living resprouts were detected (Catry et al., 2010; Lloret & López-Soria, 1993; Marais et al., 2014).

Response to herbicide surveys

Opportunistic data were collected from an uncontrolled herbicide foliar treatment of post-fire basal resprouts *of M. excelsa* by the Betty's Bay community. In this exercise, 161 resprouting individuals were treated with 10% Triclopyr during June and July 2019 (i.e., 6 months after the fire), using a knapsack sprayer. The highest concentration of Triclopyr recommended for foliar treatment of any other species for which it is registered in South Africa is 0.5% (Enviro Bio-Chem, 2018). The concentration applied in our study was thus 20 times the maximum recommended dosage. A blue dye was added to the mixture which enabled subsequent identification of the treated individuals. Treated trees were tagged shortly after herbicide treatment to enable their subsequent identification and their survival was assessed in March 2020, i.e. 9 months after herbicide treatment and thus 15 months after the fire. The pre-fire size, the fire severity experienced and the survival response of each individual were assessed in the same way as described for the post-fire survival surveys.

Data analysis

No seedlings emerged from the soil that was collected to enumerate soil seed banks and no analysis could therefore be undertaken. The data on the estimated number of seeds per tree did not conform to normality (Shapiro–Wilk $W = 0.77$, $p < 0.001$), therefore, a Spearman-rank order correlation was done to assess the relationship between the number of seeds per tree and tree height. The seed viability data did not conform to normality (Shapiro–Wilk $W = 0.83$, $p < 0.001$). Kruskal Wallis followed by multiple comparisons of mean ranks was therefore used to test whether seed viability differed between seeds from dry, green and burnt capsules. These analyses were performed with Statistica (version 13.2; Dell Inc, 2016).

To assess the prevalence of reseeding and resprouting in response to fire, we calculated the ratio of post-fire seedlings to pre-fire parents; and the ratio of the entire post-fire population (seedlings plus resprouting individuals) to the pre-fire population (Kraaij et al., 2017). To assess *M. excelsa*'s post-fire survival response in relation to fire severity and

pre-fire tree size (stem DGL), we used a logistic regression model (binomial family, logit link function) using the *lme4* package (Bates, 2010) in the open-source R software version 4.0.2 (R Development Core Team, 2019). Fire severity was treated as a four-level ordered factor (Strydom et al., 2020). We tested for collinearity between fire severity and tree size using a Spearman-rank correlation test and taking $r_s = 0.6$ as a threshold to include both fixed factors in the model (Tabachnick & Fidell, 1996). Fire severity and tree size were negatively collinear, but this correlation was weak ($r_s = -0.39$, $p < 0.001$) and both factors were therefore retained in the analysis. We used a Type II Wald chi-square test (Hastie & Pregibon, 1992) to compute the significance of fixed factors and the *MuMIn* package (Barton, 2009) to calculate conditional and marginal R^2 values. Lastly, to assess the survival of post-fire basal resprouts after herbicide application, we used a logistic regression model (binomial family, logit link), with fire severity (an ordered factor with four levels) and pre-fire size (stem DGL) as fixed factors.

RESULTS

Soil and canopy seed banks

No seedlings emerged in the germination trial. There was very strong evidence for a positive correlation between the estimated number of canopy-borne seeds per tree and tree size ($R_s = 0.45$, $n = 54$, $p < 0.001$; Figure 2). The number of seeds produced in the canopy per tree varied substantially, with an estimated average ranging from <0.5 million seeds in trees measuring 2.5 m in height to almost 23 million seeds in trees with a height of 9 m. Larger trees exhibited a greater degree of variation in seed production (Figure 2).

Viable seeds exhibited a robust staining reaction with tetrazolium chloride at a temperature of 37°C within 3 days, whereas non-viable seeds remained unstained. There was very strong evidence for differences in the viability of seeds from dry, green and burnt capsules ($H_{2,45} = 23.46$, $p < 0.001$). Viability was significantly higher in seeds from dry ($Z = 4.41$, $p < 0.001$) and green ($Z = 3.66$, $p < 0.001$) capsules from unburnt trees (median viability of 17.5%) than in seeds from capsules of burnt trees (median viability of 0.0%) (Figure 3). The viability of seeds from dry and green capsules did not differ significantly ($Z = 0.74$, $p = 1.0$).

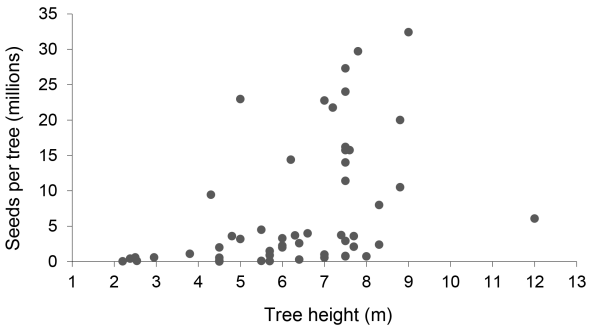

FIGURE 2 Estimated number of seeds (millions) per unburnt *Metrosideros excelsa* tree about tree height (m).

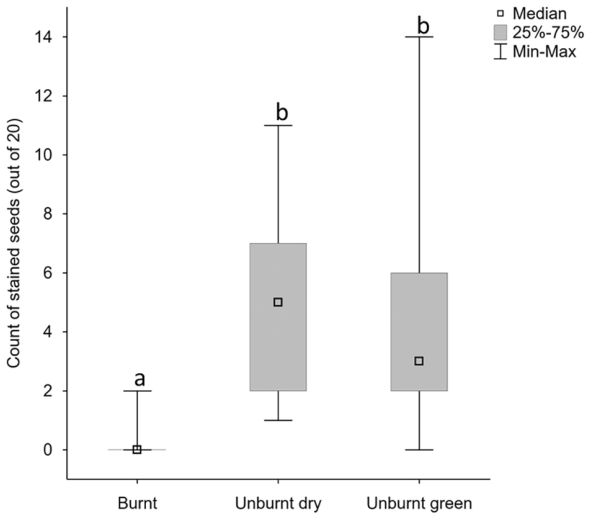

FIGURE 3 Viability of *Metrosideros excelsa* seeds from capsules collected from burnt trees compared to seeds from dry and green capsules collected from unburnt trees ($n = 300$ seeds per treatment). Different lower-case letters denote significant differences ($p < 0.05$) based on multiple comparisons of mean ranks.

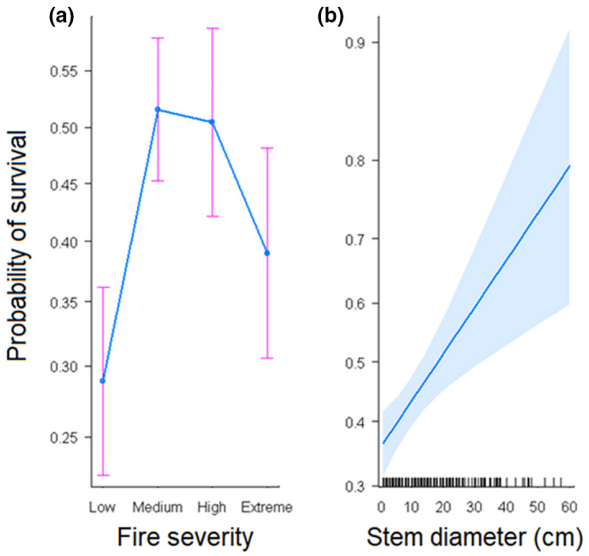

FIGURE 4 Probability of survival through basal resprouting of *Metrosideros excelsa* 15 months post-fire in relation to (a) fire severity and (b) pre-fire tree size (expressed as stem diameter at ground level). Fire severity was observed on the stem between 0 and 50 cm above ground and rated: low (bark black, but not burnt); medium (bark significantly damaged); high (wood significantly damaged); or extreme (wood severely damaged, charcoaled or burnt away). The shaded band indicates 95% confidence intervals.

Response to fire

In all the survey transects combined, only 10 seedlings were recorded post-fire, i.e., the seedling-to-parent ratio was 0.01. The post-fire survival rate of all trees ($n = 699$) was 43% and trees survived the fire through basal resprouting (Figure 1c). There was very strong evidence that fire severity affected survival rate, but in a non-linear way ($\chi^2 = 0.01$, $p < 0.001$) and that tree size had a positive effect ($\chi^2 = 0.01$, $p < 0.001$) (Figure 4). Survival rate was highest at medium and high fire severity and lowest at low and extreme fire severity. The total variance in survival rate explained by the fixed factors was 6.3%.

Response to herbicide

The survival rate of post-fire basal resprouts treated with herbicide ($n = 161$) was 9%. There was little or no evidence that fire severity ($\chi^2 = 0.77$, $p > 0.05$) or pre-fire tree size ($\chi^2 = 0.19$, $p > 0.05$) affected the survival rate of post-fire resprouts after herbicide application (Figure 5). The total variance explained by the model was 4.5%.

DISCUSSION

Soil and canopy seed banks

We found no evidence that *M. excelsa* maintains soil-stored seed banks in South Africa, consistent with transient seed banks reported for the species in its native range (Schmidt-Adam et al., 2002). It is possible that seeds were absent from the soil or that conditions required for germination may not have been met, although the latter is unlikely given that the seeds are known to germinate readily under the conditions that prevailed in the germination trial (Schmidt-Adam et al., 2002). The most plausible explanation is that seeds were no longer viable by the time they were sampled from the soil approximately 1 year after seed release, as seed viability did not exceed 1 year in the species' native range (Schmidt-Adam, 1999). Canopy-borne seeds of *M. excelsa* do not survive fire across the spectrum of low to extreme fire severity observed in the canopies and at the bases of trees at the sampling site. It is therefore unlikely that seeds of *M. excelsa* would survive fires of the severities prevailing in Mediterranean-climate shrublands. The absence of viable seeds from the burnt stand of *M. excelsa* confirmed observations from the species' native range that it depends on seeding from nearby unburnt trees (Atkinson, 2004) or resprouting (Teixeira et al., 2020) to re-establish or survive after severe disturbance.

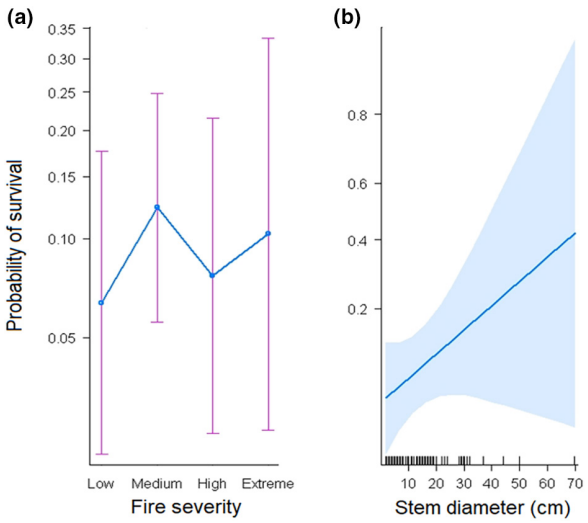

FIGURE 5 Probability of survival of post-fire basal resprouts of *Metrosideros excelsa* 9 months after foliar treatment with 10% Triclopyr herbicide, in relation to (a) fire severity and (b) pre-fire tree size (expressed as stem diameter at ground level). Fire severity was observed on the stem between 0 and 50 cm above ground and rated: low (bark black, but not burnt), medium (bark significantly damaged), high (wood significantly damaged), or extreme (wood severely damaged, charcoaled or burnt away). The shaded band indicates 95% confidence intervals.

Metrosideros excelsa (and the genus *Metrosideros* more generally) in its native range exhibits high inflorescence, capsule and seed production but with low viability (Dawson, 1968; Enright et al., 2007; Schmidt-Adam et al., 2002), although no study has directly quantified the viable seed crop of trees. We estimated that trees of various sizes produced 0.5–32 million seeds per tree, with seed production increasing with tree size; and that 18% of seeds in the canopies of unburnt trees were viable, equating to approx. 0.1–6 million viable seeds per tree. This estimate represents a vast range, while more meticulous methods, such as sampling more capsules per tree, accounting for capsule size and tree size more comprehensively and assessing variation in seed crop over time (Strydom et al., 2017; Walsh et al., 2022), should facilitate more precise estimates. There was no significant difference in the viability of seeds from green and dry capsules indicating that seeds mature early in the fruiting season and may be viable despite appearing green or immature. Our quantification of the viable seed crop of trees is crudely comparable or exceeds, estimations of the reproductive output of the species in its native range (up to 40,000 flowers per tree with 10% of ovules developing into viable seeds; Bergin & Hosking, 2006; Bylsma et al., 2014), although the measures used to express reproductive output are not directly comparable in the different studies. Nevertheless, the reproductive output of *M. excelsa* in its South African introduced range seems at least as high as that in its native range, which is to be expected given that species generally have fewer natural enemies in their introduced ranges than in their native ranges (Keane & Crawley, 2002). Although *M. excelsa* exhibits low seed viability, seeds are produced in copious quantities and with long-distance wind dispersal, the species exerts high propagule pressure which can increase the likelihood of invasion (Bergin & Hosking, 2006).

Response to fire

In its South African introduced range, *M. excelsa* survived fire surprisingly well for a species that is deemed fire-sensitive in its native range (Morrison, 2002). The post-fire population in our study was almost half as numerous as the pre-fire population, with post-fire regeneration largely accounted for by basal resprouting while recruitment from seed was insubstantial. *Metrosideros excelsa* showing some, albeit limited, capacity to regenerate vegetatively and sexually after fire, is consistent with ambiguous evidence regarding the species' adaptations (or lack thereof) to fire in its native range (Bergin & Hosking, 2006; Bylsma et al., 2014). However, our findings cast doubt over whether the capsules of *M. excelsa* protect seeds from heat and dehydration during fires and thus whether they represent a fire-adaptive trait (cf. Perry et al., 2014). The poor post-fire recruitment from seed in the study area may be owing to the absence of viable seeds from capsules of burnt trees and the lack of sufficient numbers of unburnt individuals near the burnt stand that could have seeded the burnt area. Our findings therefore support the notion that post-fire recruitment from seeds depends on seed dispersal from unburnt mature trees in the vicinity (Atkinson, 2004).

Almost half the population of *M. excelsa* survived fire through basal resprouting, with larger trees showing higher rates of survival than smaller trees. This may partly be owing to larger trees having greater root reserves to enable resprouting (Catry et al., 2010; Ordóñez et al., 2005) in addition to larger trees often having thicker bark affording better protection to the bud bank (Clarke et al., 2013; Hempson et al., 2014). A positive relation between tree size and post-fire survival has accordingly been documented

for various other tree species from New Zealand (Perry et al., 2014) and elsewhere (Giddey et al., 2022; Strydom et al., 2020). Tree survival furthermore depends on fire severity and usually, but not always, displays a negative relationship (Giddey et al., 2022; Marais et al., 2014; Strydom et al., 2020). Most New Zealand tree species are known to succumb to even low-severity fires (Perry et al., 2014) but the effects of fire severity on *M. excelsa* have not been empirically assessed before. The species has thick, flaky bark (Solangaarachchi & Gould, 2001) which is thought to make it resistant to low-intensity fires, yet susceptible to intense burning (Bergin & Hosking, 2006). This is consistent with the high mortality we noted in association with extreme fire severity. Unexpectedly, we found that *M. excelsa* survival was lowest in trees that experienced low-severity fire and propose that this anomalous result may be owing to the weak but significant negative collinearity between fire severity score and tree size. In other words, larger trees, presumably with thicker bark, were more likely to present with proportionally less damage to the bark and wood than smaller trees and fire severity in larger trees would thus more likely have been rated as relatively low.

The finding that *M. excelsa* was capable of basal resprouting after fire in its invaded South African range suggests that the species' persistence does not solely depend on seeding from individuals located outside the burnt area or a high reproductive capacity of the burnt individuals (Ordóñez et al., 2005), as is the case in its native range. We additionally observed epicormic resprouting from branches in select individuals of *M. excelsa* that occurred outside the surveyed area, a phenomenon which has also been noted in the species' native range (Bergin & Hosking, 2006; Clarkson & Clarkson, 1994). Delayed mortality after fire is a feature exhibited by some species (Lloret & López-Soria, 1993) and although we did not set out to formally evaluate this in *M. excelsa*, a comparison of a preliminary survey with our subsequent survey of resprouting suggested an extent of delayed mortality; 9 months after the fire 50% of the population exhibited basal resprouting, which declined to 43% at 15 months post-fire. It is thus recommended that survival is monitored for several years after fire (Ordóñez et al., 2005) to establish the importance of this phenomenon.

The amount of variance explained by our model assessing post-fire survival was very low (6%), suggesting that factors other than tree size and fire severity must have additionally impacted post-fire survival. These factors may include the topography, moisture and nutrient status of the soil, fire frequency, post-fire climatic conditions (e.g., amount of precipitation), post-fire competition for resources, pre-fire plant condition and age and individual plant genetics (Fairman et al., 2019; González et al., 2007; Lloret & López-Soria, 1993; Ordóñez et al., 2005). Whether the observed response was unique to the species' South African invaded range, or the context associated with the particular fire, is not known. Ideally, similar studies should be conducted across various parts of the species' introduced range and consider different fires of varying frequencies to obtain a more general perspective of *M. excelsa*'s abilities to persist through fire.

Response to herbicide

Only 9% of mature *M. excelsa* trees survived fire in conjunction with subsequent herbicide treatment of basal resprouts. This suggests that the species is sensitive to disturbances in short succession (6 months apart), akin to high mortality shown in its native range in response to frequent burning (Atkinson, 2004). The combination of burning and foliar-applied herbicide to resprouts thus seems to present a potential control method for *M. excelsa*.

It is furthermore conceivable that regular cutting or frequent burning may offer additional means of control of the species, although such approaches remain to be tested empirically. Usually, the size of woody plants influences the efficacy of herbicide treatment with larger plants often being more resistant (Enloe et al., 2018; Little, 2003). This general trend in combination with our finding that larger *M. excelsa* trees showed higher rates of survival after fire, suggests that larger individuals may generally be more resistant to disturbance. Unfortunately, given the lack of control, we could not assess mortality unrelated to the herbicide treatment. We were furthermore unable to measure the size of the post-fire resprouts at the time that they were treated with herbicide as the herbicide treatment was not planned, but the pre-treatment size of resprouts is likely to influence survival success and should be considered in control trials. The lack of a fire severity effect suggests that fire of any severity, including cooler prescribed burning, followed by herbicide treatment may constitute an effective means of control of the species.

Although Triclopyr may be a candidate for chemical control of *M. excelsa*, it was applied at an exceedingly high dosage and it is not known how effective the herbicide would be at lower dosages. However, it is imperative that herbicide application adheres to dosage guidelines to avoid increased negative impacts on receiving environments, particularly in wet environments such as where *M. excelsa* commonly occurs where amphibians are present. Treatment of post-fire resprouts should furthermore be deferred until resprouts are 0.5–1.5 m tall (Enviro Bio-Chem, 2018; Santos et al., 1992) because when resprouts are too small, the surface area of the leaves will not be sufficient to absorb the amount of herbicide required to kill the rootstock (K. M. Little, pers comm., 2019).

Management implications

Populations of *M. excelsa* can likely be extirpated due to the lack of a persistent soil-stored seed bank. If mature trees and their potential resprouts are cleared from an area, only a single follow-up removal of seedlings would be required, which should render control operations rapid and inexpensive. However, for the extirpation of populations to be successful, more information is needed on the success of seed dispersal, otherwise seemingly cleared areas may be reinfested if reproductive individuals remain in the vicinity. Given that this is an ornamental species, there may be public resistance to removing *M. excelsa* from private properties. Community engagement and education are thus key in potential control programmes for this species.

Fire may be a useful means for controlling the species as it destroys seeds and causes substantial mortality of trees and particularly of smaller individuals. *Metrosideros excelsa* exhibited low survival rates even after low severity fire suggesting that relatively safe prescribed burns may be effective to control populations. Delayed post-fire deaths occur in *M. excelsa* indicating that the survival of individuals needs to be monitored for at least 5 years after fire. It is noteworthy that the study species, in terms of its response to fire, defies the archetypal invasive species in the Fynbos Biome which is strongly fire-adapted. Accordingly, screening systems with heavy reliance on fire-adaptive traits (e.g. seed bank longevity, juvenile period, fire-survival capacity of adult plants) to identify potentially invasive alien plants in fynbos (Tucker & Richardson, 1995; van Wilgen et al., 1992) may need revision to account for species such as *M. excelsa* that clearly has different traits but also proves to be invasive in particular contexts.

Lastly, chemical control of burnt and unburnt specimens of *M. excelsa* of different sizes needs to be investigated through rigorous herbicide trials incorporating various types of herbicides at different concentrations and dosages, using diverse application methods (foliar, cut-surface, basal-bark or stream-line and basal-frill) to allow legal registration of a herbicide (Tu et al., 2001) for optimal control of this species.

AUTHOR CONTRIBUTIONS

Tineke Kraaij: Conceptualization (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (supporting); supervision (lead); validation (lead); visualization (equal); writing – original draft (equal); writing – review and editing (lead). **Sjirk Geerts:** Conceptualization (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (supporting); resources (equal); supervision (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Nicole Malan:** Conceptualization (equal); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); resources (lead); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare. The data used in this study are available on request from the authors. Permission to reproduce material from other sources was not required as none was used.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Tineke Kraaij https://orcid.org/0000-0002-8891-2869
Sjirk Geerts https://orcid.org/0000-0003-0149-2783

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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