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DISCUSSION

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Facilitating the recovery of natural evergreen forests in South Africa via invader plant stands

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Abstract

Contrary to general belief, planted and naturalized stands of introduced species facilitate the recovery of natural evergreen forests and their diversity. Forest rehabilitation actions are often performed at great cost: mature forest species are planted, while species with adaptations to recover effectively and quickly after severe disturbance are ignored; or stands are cleared of invasive alien species before native tree species are planted. By contrast, cost-effective commercial plantation forestry systems generally use fast-growing pioneer tree species introduced from other natural forest regions. Such planted tree stands often facilitate the recovery of shade-tolerant native forest species. This paper provides a brief overview of disturbance-recovery processes at landscape level, and how pioneer stands of both native and introduced tree species develop from monocultures to diverse mature forest communities. It uses one example of a study of how natural forest species from small forest patches of 3 ha in total invaded a 90-ha stand of the invasive Black wattle, *Acacia mearnsii*, over a distance of 3.1 ha at Swellendam near Cape Town, South Africa. The study recorded 329 forest species clusters across the wattle stand: more large clusters closer to and more smaller clusters further away from natural forest patches. The 28 recorded forest species (of potentially 40 species in the surrounding forest patches) included 79% tree and 21% shrub species. Colonizing forest species had mostly larger fleshy fruit and softer small seeds, and were dispersed by mostly birds and primate species. Maturing forest trees within developing clusters in the wattle stand became a source for forest regeneration away from the clusters, showing different expansion patterns. Four sets of fenced-unfenced plots in the wattle stand showed the impact of browsing by livestock, antelope, rodents and insects on the successful establishment of regenerating forest species, and the dramatic effect of excluding browsing. The results support the approach to rather selectively manipulate than clear invader plant stands in the natural forest environment. This approach invests in the natural succession process rather than planting. It protects developing seedlings against browsing by stacking invader plant debris around them, rather than protecting them by means of costly fencing. This forest recovery process through nurse stands of invasive species can be managed, with additional benefits: Indigenous tree species provide for better streambank stability; and the practice provides for local job creation over a 10-year period for harvesting poles and firewood from the manipulative conversion process.

Keywords: Browsing, Clusters, Introduced species, Invasions, Natural forests, Regeneration, Rehabilitation, Seed dispersal, Shade tolerance

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Background

Globally there is much concern, emotion and varied perspectives around plant invasions into natural vegetation systems and the threat they pose to the natural biodiversity of the systems (Macdonald et al. 1986; Henderson 2001; Kohli et al. 2009; Boy & Witt 2013). The Working for Water programme in South Africa is considered to be one of the most successful integrated land management programmes in the world (Hobbs 2004). The programme was initiated in 1995 with a modest annual budget of US$4 million. Since then, it has grown substantially; it has successfully cleared significant areas of invasive alien plant infestations, created a large number of jobs and had significant positive economic and social effects, increased water run-off into streams and reduced a major threat to the extraordinary biodiversity found in South Africa. The general aim of this programme is to clear invasive alien plants. However, the costs of controlling the plant invaders are too high to achieve the long-term goal of removing the invasive alien plants. The applied control systems often do not differentiate between the types of invader plants and the specific vegetation systems from which they need to be cleared. For instance, the same approach to clearing the invasive alien plant stands in the fire-prone grasslands and Fynbos shrublands is also followed in the shade-tolerant natural forest environment.

Contrary to general belief, planted and naturalized stands of introduced species facilitate the recovery of natural evergreen forests and their diversity (Knight et al. 1987; Geldenhuys 1992, 1996a, 1997; Parrotta 1995; Loumeto & Huttel 1997; Parrotta & Turnbull 1997; Geldenhuys & Delvaux 2007). Each natural forest area has species that function optimally in different development stages of that forest system, from pioneer stands after a major disturbance, up to mature forest (Geldenhuys 2011a). For example, the pioneer species are light-demanding, fast-growing species forming mono-specific, even-aged stands. They become gradually colonized and eventually replaced by increasingly more shade-tolerant, slower-growing species and develop towards mixed-species, mixed-age mature forest. In forest rehabilitation, we often plant mature forest species but ignore those species with adaptations to recover effectively after severe disturbance and degradation. We clear stands of invasive alien species before we plant native tree species, all at great costs, to rehabilitate natural forest. By contrast, cost-effective commercial plantation forestry systems generally use fast-growing pioneer tree species introduced from other natural forest regions.

Different situations require different solutions. What would be the ecological basis for following different approaches and practices in invasive alien plant control in natural evergreen forest, grassland or shrubland? The taller-growing invasive alien plant stands shade out the light-demanding grassland and shrubland species; they need to be removed entirely from the landscape to enable the grasslands and shrublands to recover. This is contrary to the situation in natural evergreen forest systems. The disturbance-recovery processes in natural evergreen forests resulted in different species adaptations in terms of their regeneration and establishment ecology, relative to the shady conditions of mature forest. Recovery from severe natural forest disturbances follows a successional sequence in which the early shade-intolerant pioneers in the recovery process nurse the establishment of gradually more and more shade-tolerant forest species, i.e. increases species richness of forest species. Natural forest systems have a diverse range of natural forest species that form such pioneer stands, facilitating natural forest recovery. Such systems can be sources of diverse products for livelihood needs while facilitating recovery of natural forest diversity and productivity (Geldenhuys 2013a; Mala et al. 2009). One could therefore expect differences in behavior in terms of forest recovery via shade-intolerant invasive alien plant stands. Several studies, globally, have shown the role of planted tree stands of both introduced and native species stands to facilitate or nurse the establishment of natural forest species under their canopies (Knight et al. 1987; Geldenhuys 1992, 1996a, 1997; Parrotta 1995; Loumeto & Huttel 1997; Parrotta & Turnbull 1997; Geldenhuys & Delvaux 2007). Forests also provide diverse timber, wood and non-wood products that are essential components of the livelihood needs of rural societies in many areas. Invasive alien plant stands in the natural forest environment often provide alternative resources for products in short supply from the natural forests. Clearing such invasive alien plant stands may restart the pressure on natural forest species (for poles, fuel wood, etc.) (Geldenhuys 1986, 1992, 1996a, 2002; Geldenhuys et al. 2016).

The question is therefore whether invasive alien plants pose a problem in natural evergreen forests, and if so, which particular species are causing these problems. Furthermore, if they do not pose serious ecological problems to the natural forest systems, how can their facilitation of natural forest recovery be managed? How can the options presented by the recovery process be used to develop cost-effective forest rehabilitation strategies and sustainable small business?

There may be different reasons for rehabilitating degraded or lost natural forests. One reason may be to restore their diversity per se because many floral and faunal components depend on a functioning forest ecosystem. Another reason may be to provide various resource use options for particular users who may require specific forest products, or to restore essential environmental services (nutrient cycling, carbon sequestration, soil and water conservation), or a combination of such products and services. Within a global context, there are two major concerns that underline the need for cost-effective approaches to rehabilitate natural forests. Firstly, there is the concern that natural forests are degraded through clearing for slash-and-burn traditional agriculture, charcoal production, uncontrolled timber-harvesting, and clearing for commercial agriculture, forestry, infrastructure development and mining (FAO 2003; Palm et al. 2005). Secondly, there is the concern that invasive alien plant species threaten the biodiversity and key functions of natural vegetation systems, including natural forests (Macdonald et al. 1986; Henderson 2001; Kohli et al. 2009; Boy & Witt 2013). Many invasive alien plant species are pioneer species in their native environments, and tend to function in their new environments in a similar way as the native pioneer forest species. However, they may also disrupt some ecological processes in the natural forests in their new environments, such as changing the natural regimes of gap formation (Geldenhuys 1996a), or changing the behavior of fruit/seed dispersers (Dean 1985).

Pioneer tree communities, including those composed of invasive alien species, represent specific stages in the natural development towards mixed-species, mixed-age mature forest communities (Parrotta & Turnbull 1997). The natural transition from mono-specific, even-aged stands to mixed-species, multi-age stands, includes a process of self-thinning, which may extend over long periods of time. Restoration is generally understood as anticipating a defined species composition, but this is often an unrealistic goal, because many disturbing factors are impossible to control (Aronson et al. 1993). However, the process can be facilitated to progress more rapidly. Our approach was to understand how to facilitate the rehabilitation process to advance more rapidly towards a more stable system of mixed-species, mixed-age, under various assumptions and rehabilitation goals.

The purpose of this paper is to review relevant literature on (i) the natural evergreen forests in South Africa and associated disturbance-recovery processes that determine their location patterns in the landscape, (ii) types of invasive alien plant species in the South African natural evergreen forest environment, and (iii) how stands of introduced tree species facilitate the recovery of natural evergreen forests. The paper then summarizes results from a recent study on how natural forest species invade an extensive stand of the invasive Black wattle (*Acacia mearnsii*) and how browsing by different types of animals limit the establishment success of the natural forest species. Finally, we present a decision-tree for the planning of invasive alien plant rehabilitation actions in a landscape that also includes natural evergreen forest.

Disturbance-recovery processes

Natural forest communities represent the smallest, most widespread yet highly fragmented vegetation formation in South Africa (Mucina & Geldenhuys 2006). The total area covered by forests is estimated at 3000 to 4000 km^2, i.e. less than 0.1% of the country. Most forest patches are very small (<10 ha) to small (<100 ha), occurring along the Great Escarpment, mountain ranges and coastal lowlands of eastern and southern South Africa, from 22°40′S (inland mountains) and 27°S (coast) in the northeast to 34°S in the southwest. They are embedded within a matrix vegetation of fire-prone and fire-adapted grassland, shrubland (fynbos) or deciduous woodland (Cooper 1985; Geldenhuys 1991; Berliner 2009). The forest communities contain a high plant diversity and are considered to be the second richest biome in South Africa, containing 5.35% of all South African plant species with a relatively rich 0.514 species·km^{-2}, with many widespread but also endemic/fragmented species (Mucina & Geldenhuys 2006). The use value of the forests is high in terms of timber and non-timber forest products (Lawes et al. 2004). Most forests occur in areas of high population density. Forests surrounded by affluent societies expand with little impact from infrastructural development (Geldenhuys & MacDevette 1989). Forests surrounded by developing poor rural societies are often degraded by traditional subsistence practices to satisfy social livelihood needs for building material, fuel wood, food and medicine, and other household goods (Geldenhuys & MacDevette 1989; Lawes et al. 2004; Geldenhuys & Cawe 2011).

It is often believed that natural forest communities should occur more widespread in South Africa, as well as in other African countries. The potential for natural evergreen forest presence in South Africa is limited by rainfall. Rutherford & Westfall (1986) assume a minimum of 725 mm·$annum^{-1}$ in the summer rainfall areas, and 500 mm·$annum^{-1}$ in the winter and all-year rainfall areas. Geology of the substrate generally represents no limitation to forest presence (Geldenhuys 1991; Von Maltitz et al. 2003). If one takes the 800 mm·$annum^{-1}$ rainfall boundary as reference, then about 7% of South Africa could potentially be covered by forest, but the actual forest cover is less than 0.1%. A relatively insignificant part of this disparity was caused by people clearing forest (Feely 1986; Geldenhuys 1991). Forest cover persists in landscapes with suitable rainfall and broken topography (Fig. 1). Boundaries of the very fragmented forest patches in most cases follow natural landscape boundaries. Long periods of high fire frequency caused by lightning and humans have considerably reduced the potential forest distribution to its current state. The fragmented pattern of natural forest patches within the landscape is determined by fire flow patterns related to

Fig. 1 Small, fragmented natural forest patches persist in fire-shadow areas in the landscape. These forest patches in Marloth Nature Reserve, Swellendam, South Africa, persisted when a Bergwind fire burnt back expanding forest edges

the hot, dry, gusty "Bergwinds" (low-pressure systems moving from west to east along the coastal zone) in the landscape (Geldenhuys 1994). Forest patches persisted in topographically sheltered areas and survived the wind-driven fires during the dry season. These forest patches which are surrounded by fire-adapted grassland, shrubland and woodland in the fire pathways, are potentially suitable for forest growth if fire is excluded.

It is important to note that the natural evergreen forests are not inherently resistant to fire. Occasionally during controlled block-burns in catchments of grassland and fynbos, the wind direction may change, and a forested fire-shadow area may become exposed to a fire-pathway. The mountain forests in the Southern Cape Afrotemperate forests are generally in an advanced re-growth stage, dominated by pioneer and early regrowth fire-adapted tree species (Geldenhuys 1993, 1996b). The strong, gusty Bergwinds may throw burning *Protea* flower heads, or recently also cones of invader pine stands, over distances of more than 4 km ahead of an approaching fire (Geldenhuys 2010). This may cause burnt spots inside the forest, but such spots may also be caused by lightning (Geldenhuys et al. 1994), creating a specific understory community of the fern *Rumohra adiantiformis* (Geldenhuys 1993). Charcoal of forest trees was collected below the litter layer in more than 30% of 250 plots sampled throughout the interior of the Southern Cape Afrotemperate forests (Geldenhuys 1993).

If a natural forest expands, or is rehabilitated beyond its natural 'fire shadow area', then it is likely to be destroyed during some extreme natural fire event. This happened after rehabilitation of natural forests during a 20-year observation period in the Groenkop forest near George in the Southern Cape, South Africa. This particular rehabilitation was done to extend the forest boundary to a road in order to facilitate boundary management. In one night during 1998, a Bergwind-driven fire burnt the actively rehabilitated forest back to its natural long-term boundary. The general rule for forest rehabilitation is therefore to stay outside the fire pathways (Geldenhuys 2013b). In addition, grassland and Fynbos shrubland species developed specific diverse adaptations to persist with regular fires in the fire pathways. If natural forest is allowed to expand into the fire zones, with fire protection, then such grassland and Fynbos shrubland species may be lost (with the natural forest functioning in similar ways as an invader plant community).

During the period of industrialization in South Africa, the limited natural forest resources could not satisfy the emerging timber, fibre and energy needs of South Africa. Commercial timber plantations of introduced species of mostly pine, eucalypt and acacia species were developed, which are now covering 1.266 million ha (Edwards 2011). The natural forests in many areas are surrounded by such plantations and cultivated agricultural land (Geldenhuys 2002; Edwards 2011). More than 90% of the timber plantations were planted in grassland or shrubland fire pathways. The high fire risk in these areas requires intensive and costly fire-protection for commercial forestry, agriculture, infrastructural development, and urban and rural housing. Plantations in high fire risk zones are sometimes burnt down, whereas natural forests in the fire-shadow areas not affected at all (Fig. 2).

When fire is excluded from the landscape, or cooler fires are applied during the early dry season, trees and other woody plants establish themselves within the landscape in areas potentially suitable for tree growth. Most of these trees are of pioneer-like species, often invasive alien plant species which are forming dense stands. Natural forest species also become established in areas where they did not previously grow, as can be seen on

Fig. 2 Timber plantations in South Africa are planted in grassland or shrubland adjacent to natural forest patches. They are burnt or destroyed during uncontrolled bergwind fires, with natural forest patches not affected, as at Langgewacht plantation near Kokstad

old aerial photographs dating back to the period 1938–1942. Such colonisation by natural forest species in former fire pathways has been referred to as 'naturalizing natural forest', but forest colonisation in areas where forest was cleared during recent periods has been called 'regrowing natural forest' (Geldenhuys 2011b). The distinction is important because of the legal implications for clearing of regrowing natural forest. The current regulations applied in terms of the National Forests Act of 1998 requires that no stands composed of natural forest species may be cleared, irrespective of whether they recover from destroyed forest stands or expanded into natural grassland and Fynbos shrubland by naturalization (Geldenhuys 2011b).

Invasive alien species in the evergreen forests

The number of introduced species planted in South Africa has been increasing exponentially over the years (Geldenhuys et al. 1986). European colonists settling in South Africa since 1652 brought trees, shrubs and other plant growth forms with them, planting them in their new environment to provide for timber, poles, firewood and fibre needs. Planting such species for their aesthetic value was a secondary objective. During 1985, experienced foresters at eight regional forestry offices throughout South Africa completed a questionnaire on invasive alien plants occurring in the natural forest environment in their area, specifying whether the species occur inside the forest, in forest gaps and/or along the forest margin (Geldenhuys et al. 1986). The 85 perceived invasive alien plant species were mostly just present or passive invaders, were mostly trees, shrubs and woody lianas, and very few of these species were considered active invaders under the forest canopy (Table 1). The forests were considered particularly resistant to alien plant invasion. Some species, such as pines, eucalypts, acacias and poplars, often considered active invaders of closed forest, were found to be unable to establish under those conditions. Their presence in closed forest communities was more likely the result of their establishment in former large gaps.

Most of the perceived invasive alien species are pioneer trees, shrubs or climbers in their natural environments that establish themselves on disturbed sites, in large forest gaps and along the forest margin (Table 1, Geldenhuys et al. 1986; Geldenhuys 1996a, 1997). They are generally shade intolerant and thus unable to get established under their own canopies. The fruits/seeds of many invader tree species are either small, wind-dispersed (eucalypts, pines and poplars) or have long-living hard-coated seeds (acacias, some of which are dispersed by birds, e.g. *Acacia melanoxylon*; see Geldenhuys et al. 1986; Geldenhuys 1997). By contrast, the majority of the natural forest tree species have short-lived seeds, are bird or mammal dispersed and are tolerant of shade (Geldenhuys 1996c). Several of the perceived invasive alien species have three or more uses (Geldenhuys 1986). Many are introduced commercial timber species, used in plantation forestry such as the pines, eucalypts and acacias. Several of these species have considerable use value in rural households and contribute to the conservation of the natural forest by providing essential products, such as poles, laths and firewood (Geldenhuys & Cawe 2011; Geldenhuys et al. 2016). Most of these invasive alien species facilitate establishment and growth of shade-tolerant forest species (Geldenhuys 1996a, 1997; Geldenhuys & Delvaux 2007). Invader plant control was considered to be most effective through the management of the succession process (Geldenhuys et al. 1986).

Alien communities may facilitate natural forest establishment

As mentioned before, pioneer species, in particular invasive alien plant species, usually establish themselves in dense communities in fire-prone grassland and shrubland with the exclusion of fire from the landscape. Fire exclusion happens either directly with intensive fire protection for commercial timber plantations, or indirectly through crop agriculture, infrastructure and urban development, and changed fire regimes (cool manageable fires) for grazing and conservation areas. Such

Table 1 Number of introduced species observed in the natural evergreen forests in South Africa and their invasive status, as adapted from Geldenhuys et al. (1986) and updated with current information

a) Species occurring only along forest margins and in large forest gaps	b) Species occurring along forest margins, in small and large gaps
1) 25 tree species (for some genera, individual species were not counted): Mostly passive invaders, or just being seen. More active invaders include *Acacia decurrens*, *A. saligna**, *Albizia lophantha**, *Eucalyptus* spp.*, *Melia azedarach*, *Morus alba**, *Pinus* spp.*, *Populus* spp., *Psidium cattleianum & Schinus terebinthifolius* 2) 28 Woody shrub and liana species: Mostly passive invaders, or just being seen. More active invaders include *Acacia cyclops*, *Caesalpinia decapetala**, *Chromolaena odorata**, *Lantana camara**, *Rubus niveus & Solanum mauritianum** 3) 10 Herb & soft shrub species: All passive invaders, or just being seen	1) 14 tree species: Active invaders, only in large gaps and forest margins, include *Acacia longifolia*, *A. mearnsii**, *A. melanoxylon** & *Psidium guajava** Active invaders, also under the forest canopy, include *Cestrum laevigatum**, *Cinnamomum camphora*, *Ligustrum japonicum** & *Pittosporum undulatum* 2) 7 Woody shrub and liana species: Mostly passive invaders. *Rubus cuneifolius** is an active invader, but only in large gaps and forest margins. *Dolichandra unguis-cati* & *Pereskia aculeata** are active invaders also on trees under the canopy 3) 1 soft shrub species: Just being seen

Passive invaders are able to grow and reproduce but are not dispersed widely; Active invaders are able to grow, reproduce and are dispersed widely.
*indicates widespread occurrence

naturalising stands start the recovery process through natural succession. The dense monospecific, shade-intolerant, pioneer tree (nurse) stands become 'invaded' by shade-tolerant forest species as the nurse stand develops and naturally undergoes self-thinning (Fig. 3). As the nurse stand matures and becomes less dense, more shade-tolerant natural forest species of middle to late successional stages become established and an increasingly more diverse regrowing natural forest develops (Geldenhuys 2009).

Planted and naturalizing stands of shade-intolerant introduced tree species of pines, eucalypts, acacias and other species facilitate the establishment of shade-tolerant native forest species, with the development of alien plant communities (Knight et al. 1987; Geldenhuys 1992, 1996a, 1997; Parrotta 1995; Loumeto & Huttel 1997; Parrotta & Turnbull 1997; Geldenhuys & Delvaux 2007). These studies show variation in species composition and density with different nurse stand species, density of the nurse communities and development over time, and in response to the distance from the seed source of a natural forest stand. Such nurse communities may buffer the more variable and extreme conditions of regularly disturbed grassland, shrubland and agricultural cropland, and add litter to the site that ameliorates the nutrient and moisture content of the upper soil layer. This is a typical succession process which could take many years towards recovery of the mixed species mature forest community (Geldenhuys 1994). The forest succession process through the nurse communities can be manipulated through selective thinning to speed up the recovery towards mixed-species natural forests at relatively low cost (Fig. 3; Geldenhuys & Bezuidenhout 2011; Geldenhuys 2013b).

Case study: Buffeljags River

Two specific ecological studies were conducted at Buffeljags River, near Swellendam, South Africa, on the rehabilitation of alien invaded riparian zones and catchments using indigenous trees (Everson et al. 2016).

The purpose of the research was to understand the local invasion process and to achieve a successful establishment of the colonising forest species. The study site was a 90-ha community of *Acacia mearnsii* (Black Wattle) trees, extending for 3.1 km between the Buffeljags River and the Langeberg Mountain range to the north (Fig. 4). Several small patches of moist, dry and riparian forest occur at the upstream end of the wattle community, covering about 3 ha. The wattle community was cleared prior to 2004, but then developed more extensively and densely afterwards, regenerating from long-living seed banks in the soil.

Assessing the invasion and establishment potential

The first study was designed to assess the invasion and establishment potential of specific natural forest species within the wattle community (Atsame-Edda 2014; Everson et al. 2016, Everson et al. 2016b). The hypothesis in this study was that the primary invasion process is initiated through seeds dispersed from outside the wattle stand, from the forest patches, causing the establishment of forest tree clusters within the wattle stand. This process is then followed by a local expansion emanating from the established tree clusters into uninvaded areas within the wattle stand. In total, 329 clusters of natural forest species were mapped throughout the wattle stand: 266 small clusters (containing 1–3 reproductively mature trees) with 53% in the distant zone, 36 medium-sized clusters (4–9 trees) with 77.8% in the proximity and intermediate zones, and 27 large clusters (10+ trees) with 59.3% in the proximity zone (Table 2). Large clusters were especially abundant in close vicinity to the natural forest patches while small-cluster numbers increased with increasing distance from the forest patches, representing an active invasion process.

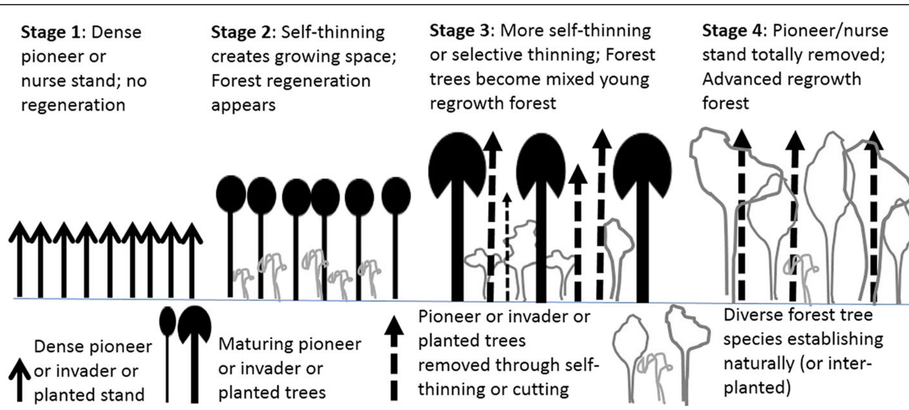

Fig. 3 Conceptual model of the relationship between stand development stage and the establishment of understorey vegetation of natural forest tree regeneration (adapted from Geldenhuys 2013b)

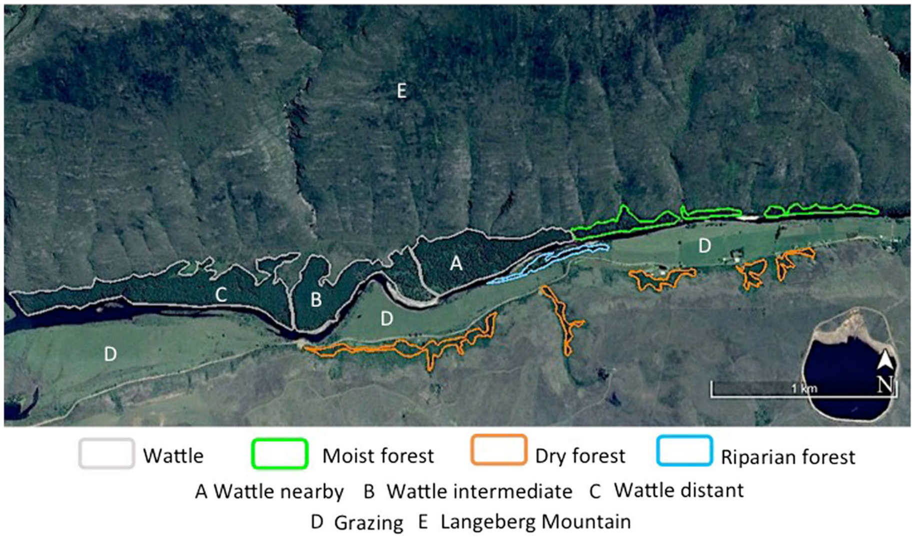

Fig. 4 Distribution of the Black wattle (Acacia mearnsii) stand (3.1 km long, covering 90 ha) at Buffeljags River, near Swellendam (South Africa) in relation to the distance to moist and riparian forest patches to the eastern upstream (right) end, and dry forest patches across the river to the south (adapted from Atsame-Edda 2014). Note that the Wattle stand was zoned, for this study, into nearby (A), intermediate (B) and distant (C) wattle areas, in relation to the natural forest patches. South of the river the alluvial terrace was used for grazing by cattle (D). The Langeberg mountain (E) is covered by the fire-prone Fynbos shrubland)

Of the 40 tree and shrub species recorded in the forest patches, 28 species belonging to 20 families were recorded in the forest clusters. Five tree species were common throughout the wattle stand up to its western end: canopy species White stinkwood (*Celtis africana*), Cape beech (*Rapanea melanophloeos*) and White ironwood (*Vepris lanceolata*), and sub-canopy species Turkey berry (*Canthium inerme*) and Spike thorn (*Gymnosporia buxifolia*). Riparian forest was the primary seed source of establishing forest clusters, but moist and dry forest patches also contributed species to forest cluster development. Some larger clusters included large trees of common species, suggesting that they could have been part of remnant forest patches from an earlier forest clearing (Atsema-Edda 2014).

Secondary forest expansion within the invasive alien plant stands took place through local cluster expansion in all directions from reproductively mature trees of well-established clusters. Fruit/seed characteristics and dispersal mechanisms of most species in the establishing clusters and observations on site suggest that Rameron pigeons (*Columba arquatrix*), Red-wing starlings (*Onychognathus morio*) and Chacma baboons (*Papio ursinus*) were the main fruit/seed dispersers. The following patterns were observed in terms of species inside a cluster, and species of regeneration outside the clusters (Atsema-Edda 2014):

- Dominant species in the surrounding regeneration had an adult tree within a cluster, such as *Celtis africana*, *Rapanea melanophloeos*, *Vepris lanceolata* or *Maytenus acuminata*;
- Dominant species in a cluster was not dominant or was absent in the surrounding regeneration;
- Some species were present in the regeneration zone outside a cluster and were absent from the tree cluster

Table 2 Distribution of small, intermediate and large clusters of natural forest species in the nearby, intermediate and distant zones (Fig. 4) of the Black wattle (*Acacia mearnsii*) stands at Buffeljag River study area

Acacia meanrsii zone	Zone area (ha)	Total number of clusters	Cluster size (stems of natural forest species)		
			Small (1–3 stems)	Medium (4–9 stems)	Large (10+ stems)
			Number of clusters		
Nearby	30	94	62	16	16
Intermediate	20	81	63	12	6
Distant	40	154	141	8	5
Total	90	329	266	36	27

Regeneration density at distances of 6, 12 or 18 m away from a cluster also showed three different patterns (Atsema-Edda 2014):

- decreased with increasing distance away from cluster;
- increased with increasing distance away from cluster;
- showed no pattern away from cluster.

Assessing the impact of browsing

The second study was designed to assess the impact of browsing on colonising forest seedlings within the wattle community (Everson et al. 2016). Cattle from across the river were a major constraint to a successful conversion process. This study used (a) a fence between the river and the wattle stand to exclude cattle from most of the area, (b) four small fenced plots to exclude small antelope such as bushbuck (*Tragelaphus scriptus*) and duiker (*Sylvicapra grimmia*), with a non-fenced plot outside each fenced plot as a control (established in March 2013), and (c) manipulation of the developing dense ground cover of a scrambling, semi-succulent *Commelina* species inside fenced plots to reduce hiding places for vlei rats (*Otomys irroratus*). The eight fenced/unfenced plots included 297 forest seedlings of 10 woody species. The cattle and antelope browsed the leaves and shoots of the establishing forest seedlings (Fig. 5a). The vlei rat either removed the bark from the lower part of the seedlings (Fig. 5b) or cut the stems just above the ground. Unidentified insects browsed the growing tip of only one species (*Gymnosporia buxifolia*). Fencing and the stems of fallen wattle protected establishing forest seedlings so that they could quickly grow beyond the browse height of cattle and antelope (Fig. 5c, d). Removal of the dense herbaceous *Commelina* species caused the retreat of the vlei rat. The browsers acted species-specifically. The browsing led to reduced plant vigour and height growth, distorted plant form and seedling deaths. Browsing by cattle, antelope and rats delayed successful establishment and growth of forest tree seedlings for more than 12 years. Browsing impacts can be reduced through fencing, but also through stem/branch stacking around developing seedlings.

Management aspects

In fire-adapted systems, the invasive alien tree and shrub species compete directly with the shade-intolerant grassland or shrubland species. Here the invasive alien species need to be cleared or eliminated before the natural vegetation systems and species can recover. A different approach is required in the natural forest environment because such clearing of the alien cover will keep the stand development in stages 1 and 2 (Fig. 3), i.e.

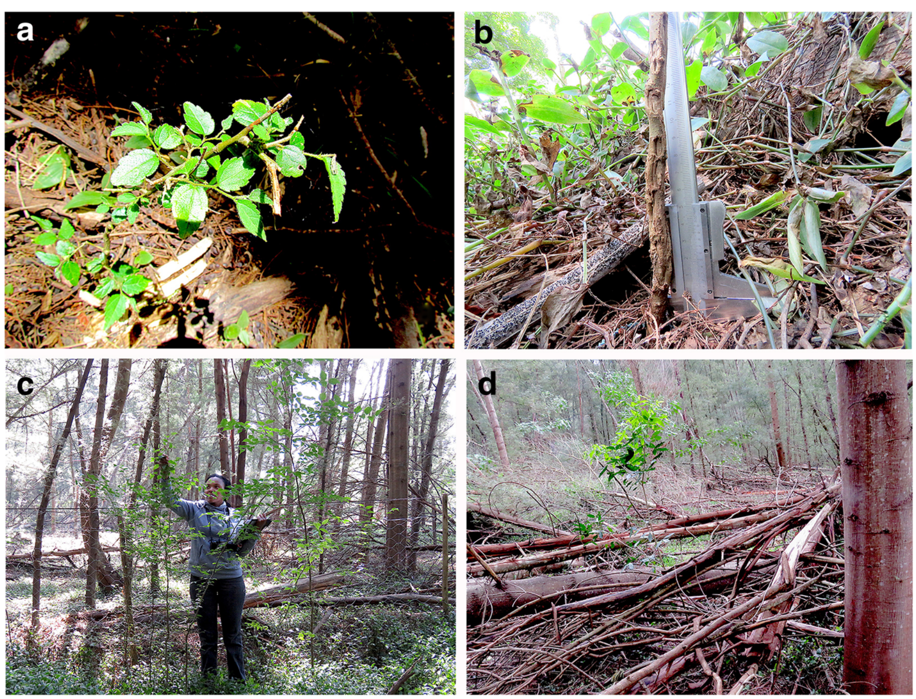

Fig. 5 Browsing impacts and approaches to protect seedlings against browsing: (**a**) Cattle and antelope, mainly Bushbuck (Tragelaphus scriptus), browsed the leaves and new shoots of seedlings; (**b**) Vlei rat (Otomys irroratus) removed the bark of the seedlings but also removed the upper part of the stem as if it was cut with a pruning scissor; (**c**) Inside the fenced plots, seedlings grew up to >3 m height since establishment of the fence in 2013; (**d**) Seedlings grew fast in height between the cut stems of wattle trees

perpetuate the invasion problem. A manipulative selective thinning of the stems of invasive alien plant stands has been advocated as a more cost-effective and long-lasting approach to the conversion of such stands to natural forest (Geldenhuys & Bezuidenhout 2011; Geldenhuys 2013b). The cover of the nurse stand systems (particularly the alien tree cover) can be removed from the system through gradual thinning of the nurse stand (Stages 2 & 3 in Fig. 3) until no more alien trees are present (stage 4 in Fig. 4). This management approach is possible because most alien 'invaders' are shade intolerant (nurse stands) but most natural forest species are shade tolerant. The nurse stand therefore facilitates the recovery of the natural forest system and species.

Clearing alien invaders and subsequent planting of indigenous tree species to rehabilitate natural forest is expensive. Personal practical experience of such a planting action in different areas has shown that natural regeneration outgrew the planted seedlings. Planting of indigenous tree or other species within the regrowing forest system will only be necessary for species that would not easily disperse there.

The areas with stands of invasive shade-intolerant species are usually grassland/shrubland that became invaded by alien tree stands because of a lack of fire, with possibly some areas of a degraded forest. Some of the invader plant stands have to be restored to productive land use, grassland or shrubland (mostly in the fire zone) and in the forest environment have to be restored to forest (in the fire-shadow areas). The rehabilitation area needs to be managed in four steps (Geldenhuys & Bezuidenhout 2011; Geldenhuys 2013b; Everson et al. 2016).

Step 1: Broad zonation of rehabilitation area in terms of the end-points in alien tree removal, such as productive farmland, continued timber production areas, broader riparian zones, and stream bank areas. Everson et al. (2016) developed a decision-tree to guide the active rehabilitation of invasive alien plant communities (Fig. 6). The proposed activities differentiate between a) areas that need abrupt and complete clearing of alien vegetation in native grassland or shrubland, and b) areas where gradual removal of alien communities is preferred, e.g. in 'novel forests' or riparian tree communities. The aim is to maintain a spatial mosaic of natural forest areas, other plant communities and developed land. Rehabilitation should be confined to 'fire-shadow' areas which are located outside of the fire pathways, unless the area is within a built-up environment or agricultural land or a commercial forestry estate which is directly or indirectly protected against fire. In terms of the fire patterns (Figs. 1 and 2), the riparian/riverine zones in a potential forest environment could be considered 'forest' zones. In natural areas the conversion should be confined to areas near the forest margin or on sites that had been cleared of forest. Changed fire regimes and extensive areas of invasive alien species have made natural forest boundaries within fire shadow areas less clear. Good quality aerial photographs have been available for most of South Africa since the 1940's, and could be used to determine safe sites for forest rehabilitation. Other conversion

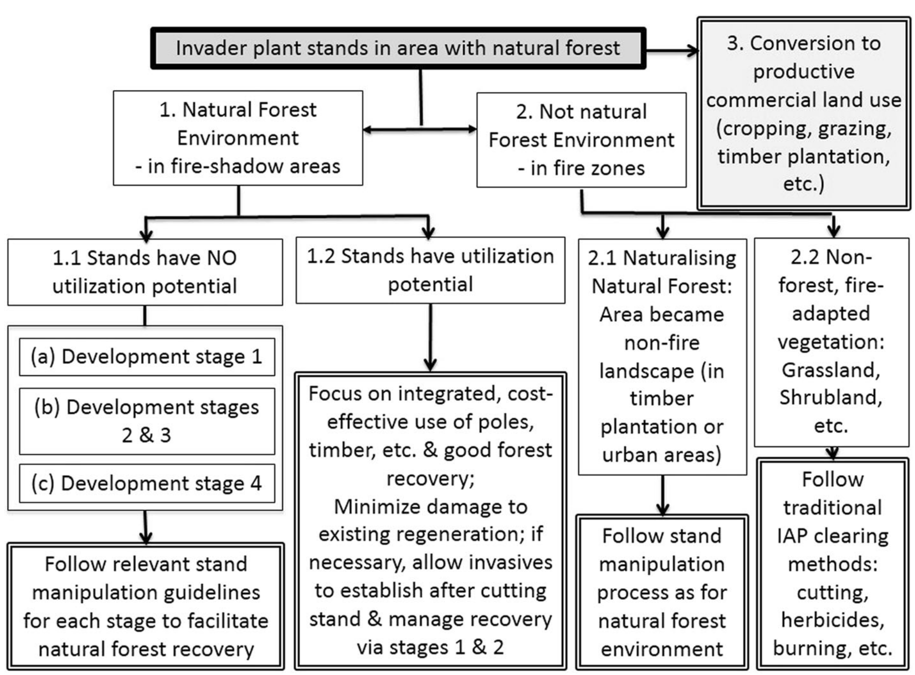

Fig. 6 Decision tree to decide on rehabilitation action for invader plant stands in different vegetation systems (adapted from Everson et al. 2016b)

constraints and rehabilitation costs should be determined for the different forest areas. In some areas it may also be necessary to determine the needs of specific stakeholders for potential species (forest, shrublands, other land uses) through surveys to adapt the rehabilitation activities. For example, poles of alien invader trees could be used for house construction in rural areas or for making small garden chairs for sale in urban areas as small enterprises. Some regenerating forest species could be used for traditional medicine requiring particular attention by management in the rehabilitation process.

Step 2: Zone the 'forest' and riparian sites identified for rehabilitation to regrowth natural forest, by stand development stages (see Fig. 3). The criteria used for the differentiation include stands of different overhead composition (species) and 'age'(size) and development stages of the indigenous woody vegetation in the understorey. The following criteria have been developed for assessment of the stand development stages in the natural forest zone (Geldenhuys & Bezuidenhout 2011; Geldenhuys 2013b):

Development stage 1: Dense, young nurse stands with many small stems of the nurse stand species, including stunted and suppressed stems. Gradually, as this stand grows taller, many stems die because of competition from the faster-growing stems. Very few to no indigenous tree species, or scattered individuals that existed before, may be present. Manual stand manipulation needs to be delayed until the stand develops through self-thinning. Where forest tree seedlings and saplings do appear, some invader plants can be removed (hand pulled, cut or ring-barked). The stands need to be inspected from time to time.

Development stage 2: The nurse stand is still relatively dense, but taller. Forest tree seedlings and saplings and species of other growth forms start to establish in the understorey, sometimes in small clusters. These species often include shade-tolerant tree species from a nearby natural forest, but they are small and develop slowly because of the relatively low light conditions, even though they are tolerant of some shade. The focus in stand manipulation should be on selective removal of invader plants around establishing natural forest seedlings to facilitate their growth into saplings and poles.

Development stage 3: Natural stand thinning is in progress. More stems of the nurse stand die back to create more space in the understorey, with more light. This allows the development of more forest tree clusters and the development of the establishing natural forest tree species into young tree stems amongst the fewer nurse stand trees. Tree clusters expand laterally with new plants establishing away from the cluster core. The focus in stand manipulation should be to remove all nurse stand plants within the clusters and to create just enough open space adjacent to the cluster to facilitate expansion of the cluster.

Development stage 4: This is the advanced stage of forest recovery, with most or all of the nurse plant stems removed (or dead). The forest structure is developing towards a continuous forest canopy and tree stems are found in a range of stem diameters as more species become established and the young stems grow into trees and into the canopy. At this stage the stand conditions are such that shade-intolerant invader plant species cannot establish, even if they are present in small numbers in the understorey. The focus in stand manipulation should be to remove all invader plants in a gap, or on the forest edge. It is a low-intensity activity that requires an occasional inspection to remove alien trees that may establish in gaps. Such stands could be used as a norm for recovery of stages 1 to 3.

Step 3: Implement stand manipulation in stand development stages 2 and 3. The intensity of rehabilitation activities will vary according to the development stage (canopy and understorey) of each nurse stand. Selected unwanted trees of the nurse stand should be gradually removed with care to enable the regeneration of natural forest species to become established naturally. The selected stems could be cut for direct use or ring-barked to die standing in the selective thinning (not clearing). Six golden rules need to be considered:

1) The focus should be on the establishing forest species clusters;
2) A relatively closed nurse stand canopy should be maintained to prevent regeneration and regrowth of the nurse stand species. It should be opened above forest species clusters to help the forest seedlings, saplings and poles to grow stronger, and to flower and fruit earlier to enable fruit/seed dispersers to help with the process;
3) Small suppressed or stunted sub-canopy stems of the nurse stand species should be removed to provide more growing space for the regeneration and growth of forest species in the understorey;
4) The ground cover (herbaceous plants, litter, dead branches, etc.) should be kept intact to prevent invader or pioneer species from establishing. However, when the ground cover becomes too dense and high to exclude seedling establishment and growth, and becomes a shelter for rodents, it should be carefully removed.
5) Tree debris should not be burnt on the rehabilitation site: the generated heat will a) kill seeds of forest species that may be present in the organic and/or litter layers; b) destroy the soil organic layer and associated micro-organisms involved in the decomposition and nutrient cycling processes (sterilize the soil); and c) stimulate hard-coated seed of particularly invasive *Acacia* species to

regenerate in mass. This will push the recovery process back for several years.

6) Woody stems should be stacked around developing seedlings to protect them from being browsed by livestock and antelope. The stacks should be at about 1 m or more from the developing seedlings and saplings to prevent antelope to reach the forest plant.

This general process facilitates the conversion of an alien community to a natural forest through selective removal of the invading nurse trees, when the nurse trees have relatively small stem diameters. However, sometimes the nurse stand is composed of large, branchy and useful trees of one or more alien tree species that could be used for timber, poles, fuelwood or charcoal (Geldenhuys & Bezuidenhout 2011). The first priority would then be to remove all utilizable stems before the rehabilitation actions are implemented. The non-harvestable tree debris could be left on site but in sections not longer than 2 m (as bird perch sites, as micro-sites for seedling establishment and small animals and micro-organisms, to protect seedlings against browsers, and as a slow-release 'fertilizer' through natural wood decomposition). However, if such an alien tree stand grows inside the riparian zone or on the banks of a river, then the first priority would be the safety and security of the river in terms of people's lives, infrastructure (bridges, pipelines, water pumps, etc.), and ecotourism activities on and along the river. Then all alien trees should be removed in one action to prevent stream blockage during flooding, by drifting branch wood and deformed non-harvestable main stems, which may cause associated increased flood levels and infrastructure damage. If good native forest regeneration were present in such an alien tree stand, then care should be taken to minimize damage to the native tree regeneration by the falling cut nurse stand trees. But even if the native tree regeneration is damaged by the cut trees, then most of the regenerating woody species will recover through relatively fast vegetative regrowth. In this latter case of removing large tree debris along the river, the non-harvestable tree debris could be burnt on site with care to keep the burnt spot footprint small and to prevent scorch of the regenerating plants of native woody species.

Step 4: Planting of forest seedlings should be limited to spots in the stand with no forest seedlings or to specific species that do not disperse easily. Seedlings could be collected from clusters of seedlings (maximum 50% of the seedlings in dense clusters) from the nurse stand, drainage lines along local roads, or the nearby natural forest. Such planting should be done during misty or rainy weather to ensure success. Where tree debris was burnt, it is necessary to wait until the ash bed has cooled down, and cover the burnt site with sods of top soil and small plants from the areas around the burnt spot to ensure rapid recovery.

Conclusion

Natural pioneer and introduced plantation/invader species can become a partner in forest rehabilitation towards recovery of biodiversity and productivity. The natural succession process with the invasive alien plants as the pioneer nurse stand can be used to reduce costs. The aliens provide a rapid ground cover, which prevents erosion, adds litter to a degraded site which would help to restore nutrient cycling and increase the moisture content of the growing medium. The nurse stand provides shade and reduces strong wind to facilitate the establishment of shade-tolerant natural forest species and thereby recover the biodiversity as in any native pioneer stand. The results from the various rehabilitation actions according to this particular manipulative approach have shown that a pioneer or planted or naturalized nurse stand can be converted to natural forest, cost-effectively, if it is not in the normal fire zone. The manipulative 'interference' through selective thinning facilitates and speeds up the development towards a natural forest community. A practice of repeated clearing of invader plants, for example in the riparian zone, can be turned into a system of regrowing forest with highly reduced maintenance costs. The removed stems could be used for laths, poles, firewood, timber, depending on the development stage of the nurse stand. Medicinal plant crops and other forest species could be harvested from such stands (Geldenhuys & Delvaux 2007). The practice therefore provides options for small business development parallel to the rehabilitation process. This new approach requires a different mind-set providing a variety of benefits to the owner of the land, as well as adjacent communities in many areas.

Shade-tolerant invasive alien plants require different approaches (Geldenhuys 2011c). For such species, it is important to remove the seed source by ring-barking the mature trees. In the case of the climbing cactus, *Pereskia aculeata*, the entire host tree has to be removed, and all material of this species needs to be burnt on site to prevent vegetative regrowth. The basal parts of the climber *Dolichandra unguis-cati* need to be cut so that the stems in the crowns die. It is a much more complex action, but in most cases the problem is relatively confined to groups of trees.

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Authors' contributions
CJG developed the concept over time and guided the specific research on the experimental part reported on. AA-E did the study on the forest species invading the invader plant stand and completed her MSc study on it. MWM did the study on the browsing impacts and is still busy with writing up her MSc. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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