

The invasive *Melia azedarach* in Durban (South Africa): impacts on tree community structure

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Abstract *Melia azedarach* L. (Meliaceae) is an invasive, rapidly growing tree, considered one of the most important transforming invasive alien plants in South Africa. Here we survey several localities across the city of Durban (eThekwini Municipality in the province of KwaZulu-Natal), with and without adult *Melia* trees, including indigenous trees, as well as other alien species. Notwithstanding significant differences between localities, we find that localities

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P. R. de Moura Souza-Filho Centro Multidisciplinar de Barra, Federal University of Western of Bahia, Barra, Bahia 47100000, Brazil with adult Melia trees have substantially reduced tree species richness and marginally smaller tree diameter at breast height (values combining indigenous trees, Melia, and other alien trees). The composition of adult tree assemblages differs considerably from the composition of tree seedling assemblages at most localities, with Melia seedlings present at all localities, irrespective of the presence of adult trees. The differences between adult and seedling communities are more pronounced where adult Melia trees are absent, indicating rapid transformation due to incipient invasion. This also suggests that Melia dominance may cause long-lasting vegetation uniformity and that the transformation process caused by the alien trees at these localities is already somewhat stabilized. We discuss the implications of Melia presence and local dominance on the local ecosystems and suggest controlling this species at target localities of conservation relevance.

Keywords Plant diversity · Seedlings · Tree population structure · Urban tree invasions

Introduction

Melia azedarach L. (Meliaceae), locally known as 'syringa' in South Africa, an alien tree growing up to 20 m, is assumed to have been introduced to the country from northern India in the early 1800s (Smith 1966; Mabberley 1984). It has since become highly

invasive in the warm eastern and northern parts of the country (Henderson 2001; Voigt et al. 2011; Richardson et al. 2020) and is now listed as one of the top ten invasive plants in terms of the area it covers (Van Wilgen and Wilson 2018). Melia azedarach (hereafter Melia) trees have fast growth rates, are prolific seed-producers and can regenerate via coppicing. They can grow under a variety of conditions and invade naturally and anthropogenically disturbed habitats along with river courses, roadsides, as well as in urban open spaces, but they also grow in undisturbed savanna and woodland fringes (Henderson and Musil 1984; Bromilow 2001). The species is currently categorized as a '1b invasive alien plant species' (meaning that it is on the compulsory control list) and falls under Category 3 in urban areas (cannot be kept without a permit, and certainly not in riparian zones; see Department of Environmental Affairs (South, Africa) 2016, for details on category criteria). In some limited areas, this species has already outcompeted the majority of the species from the original native vegetation in terms of total cover and biomass (Gairola et al. 2016). In the future, it will, in all likelihood, become one of the dominant species over broader scales in new emerging vegetation types characterized by novel ecosystem processes (Padayachi et al. 2014; Procheş et al. 2015).

Melia impacts the functioning of South African ecosystems in numerous ways. It has the potential to influence the trophic structure of invaded ecosystems; for example, birds that disperse Melia seeds may ignore the fruit of previously dispersed indigenous trees (Voigt et al. 2011). By suffering greater mistletoe infestation than most indigenous woody species (Gairola et al. 2013), it increases mistletoe abundance, altering overall vegetation composition and structure. However, in South Africa and globally, the literature on the Melia invasion and its impacts on vegetation structure and composition or on biodiversity as a whole is surprisingly limited. To our knowledge, no study has specifically focused on how the invasion of this species is actually affecting tree species regeneration and species composition.

In order to obtain detailed insights into the effects of this invasive species on native communities, its impacts on species richness, diversity, abundance, evenness, population structure and dominance need to be examined in detail. In this study, we analyse the impact of *Melia* on patterns of understorey seedling diversity and density in woodland patches in the Durban area (the eThekwini Municipality, KwaZulu-Natal, South Africa), where the species has been present for a long period of time, and discuss strategies for the management of this species. We hypothesize that tree community variables such as species richness and population structure have been negatively affected by Melia. We also compare the adult tree and seedling assemblages as an indication of community dynamics.

Material and Methods

Study Localities and Vegetation Sampling

The Durban (eThekwini) Municipality is located on the east coast of South Africa, in a subtropical climate with rainy summers and relatively dry winters. The vegetation is represented by a patchwork of woodland, savanna and grassland, labelled as the Indian Ocean Coastal Belt (Mucina and Rutherford 2006). We established sites at five localities within parts of the eThekwini Municipality with naturally woody vegetation (Table 1). The sites were not selected randomly, given the steep terrain characteristic of much of the Durban areas, and also because of safety concerns; however, they were spread as possible within the central part of the municipality

Table 1Localitiessurveyed within theeThekwini Municipality		Site	Habitat	Number of plots	Elevation [m a.s.l.]	GPS coordinates
	Westville North	1	Pristine River Valley	20	237	29.81° S, 30.93° E
	Palmiet	2	Nature reserve	20	100	29.82° S, 30.96° E
	Clermont	3	Gorge	18	287	29.80° S, 30.90° E
	Sydenham	4	Disturbed site	14	252	29.88° S, 30.99° E
	Glen Hills	5	Pristine passive recreation site	10	96	29.76° S, 31.04° E

as far as these practical considerations allowed. The area of the localities was 2 to 10 km², and all localities contained substantial areas of Melia invasion, but also easily identifiable adjacent areas with similar natural vegetation and soil types that had no adult Melia trees (but did harbour Melia seedlings, as well as other invasive species, see the Results section). All study localities appeared to be invaded by Melia for many years based on tree sizes, although the estimated age of invasion at each site was not available. Fieldwork was conducted throughout 2012. We established 10×10 -m plots at each of the five localities. Half of the plots were in areas with adult Melia trees and the other were in areas without them; however, the total number of plots varied for each locality (see Table 1). Localities without adult *Melia* trees were at least 50 m but not further than 70 m from the nearest adult Melia tree, as much as this was feasible at each site given the topography. This distance was dictated by the requirement to best represent the only moderately transformed vegetation characteristic of the locality while being comparable with their immediate Melia-invaded, more severely transformed, counterparts. Plot selection was made in a manner meant to best approximate random selection while taking into consideration that, in some cases, the steep terrain constrained choices substantially. Within each 10×10 -m plot, we recorded the species and diameter at breast height (DBH) for all the present trees. Tree seedlings were counted in two 1×1-m quadrats per each 10×10-m plot. Individuals of all species were identified in the field whenever possible; samples of unidentified species were brought back to the laboratory and identified using field guides (e.g. Boon 2010; Pooley 1998; Van Wyk and Van Wyk 1997) and Ward Herbarium (UDW) records. The nomenclature and taxonomic authorships follow the NEW Plants of Southern Africa (NEWPOSA) website of the South African National Biodiversity Institute (SANBI 2018).

Data Analysis

Species richness, the Shannon–Wiener index and Simpson's index were computed for each 10×10 -m plot, and the DBH of trees inside these was measured. These data were then compared within the localities for the presence of adult *Melia* trees using linear

mixed models (LMM) with the presence of *Melia* in the plot as a fixed effect and the localities as a random effect (IBM Corp 2016). This type of modelling was preferred to deal with the unbalanced design from plots. Then we performed the Wald chi-square test to evaluate the effect of the presence of *Melia*. The diversity indices were computed with the 'vegan' package (Oksanen et al. 2019), the LMM were built with the 'lme4' package (Bates et al. 2015) and the Wald chi-square test performed with the 'car' package (Fox and Weisberg 2019), all in R (R Core Team 2019).

To compare tree and seedling assemblages and the effect of the presence of Melia, we used the multivariate statistical package 'mvabund' (Wang et al. 2012; Wang et al. 2020). For modelling, the total number sampled of the adult trees and seedlings(i.e. plant stages) and the presence of Melia were analysed. We fitted a negative binomial model for counts and performed analysis of variance and usin Wald statistics with 999 resamples. In addition, we performed nonmetric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity index to visualize the relationships between the assemblages of adult trees and seedlings. We removed the *Melia* from that analysis. We used the abundance of the sampled plant stages at the localities, and at each plot, with and without Melia to determine its communities and visualize it relations.

Results

A total of 59 tree species were found at all localities as adults (Appendix Table 3). All but eight of these and a further 14 species were found as seedlings (Appendix Table 4). Nineteen of the species from the combined adult/seedling list were aliens, including some notable widespread invaders such as *Litsea glutinosa* (Lauraceae), *Morus alba* (Moraceae), *Solanum mauritianum* (Solanaceae) and *Tecoma stans* (Bignoniaceae), but most of them were locally distributed emerging invaders. Not recorded in our plots but present at the localities were a variety of invasive shrubs, vines and herbaceous plants, including important invasive species such as *Lantana camara* (Verbenaceae), *Chromolaena odorata* (Asteraceae) and *Cardiospermum grandiflorum* (Sapindaceae). All of the species listed above occurred as both adult plants and seedlings at least some of the localities (for details on the representation of tree species, see Appendices Tables 3 and 4). Among trees, *Melia* was the most common alien species overall, dominating at four of the five localities (*Morus alba* being dominant at one locality). *Melia* seedlings occurred in plots both with and without adult *Melia* trees at all the five study localities. For all localities, the number of *Melia* seedlings was always greater in plots with

Table 2 Analysis of deviance table with type-II Wald chisquared tests for adult tree sampled in 10×10 -m plots: species richness, Shannon–Wiener index, Simpson's index and diameter at breastheight for the effect of the presence of adult individuals of *Melia azedarach*

Effect	Wald χ^2	D.f	Р
Species richness			
Melia presence	82.889	1	< 0.001
Shannon-Wiener ind	lex		
Melia presence	26.472	1	< 0.001
Simpson's index			
Melia presence	27.398	1	< 0.001
Diameter at breast he	eight		
Melia presence	6.4998	1	0.011

Melia trees. Localities with adult *Melia* trees had 13.4 ± 5.6 species present as adult trees and 17.4 ± 7.2 as seedlings; those without adult *Melia* 20.6 ± 9.1 species present as adults and 21.8 ± 6.3 present as seedlings (mean \pm standard deviation). In every single plot, both alien and indigenous adult trees and seedlings were present, although no significant differences could be found in the proportional representation of the two categories of species between plots with and without adult *Melia* trees; for this reason, the other adult invader plants were not affected by the presence of *Melia* (Wald $\chi^2 = 0$, P = 1).

For four of the five localities, were adult individuals of *Melia* were absent from the plots, the total number of species was significantly greater compared to plots in which adult *Melia* trees were present (Table 2, Fig. 1). The number of adult tree species, both alien and indigenous, (i.e. richness) varied between plots with and without the presence of adult individuals of *Melia* (Table 2). The diversity was also affected by the presence of *Melia* (Table 2). The mean Shannon–Wiener diversity index dropped from $H'=1.4\pm0$ (without *Melia*) 4 to $H'=1.0\pm0.4$ (with *Melia*). Simpson's index of similarly decreased from 0.7 ± 0.2 without to 0.5 ± 0.2 with *Melia*.

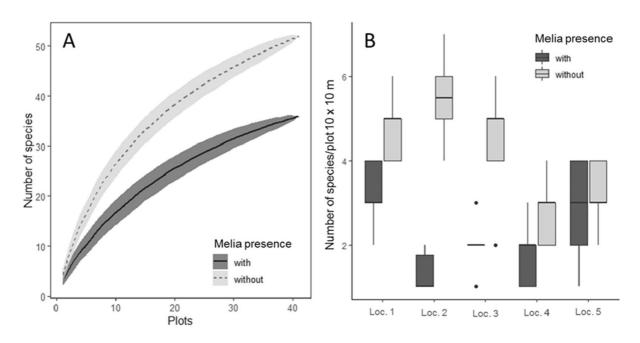


Fig. 1 A – Curve of tree species identified in each of 10×10 plots with or without *Melia* trees and B – box-plot for the number of species for each of the five study localities with or without adult *Melia* trees

The DBH of trees in the plots with and without adult individuals of Melia was slightly significant (Wald $\chi^2 = 6.49$, P = 0.01, Table 2); at locality 5 this value was considerably greater in the plots without adult Melia (Fig. 2).

In the NMDS ordination diagram, visualizing community composition similarity across all localities (Fig. 3), there is a broad scatter of points representing localities with and without adult Melia trees. Locations with Meila tend to be left positioned in relation to those without Melia. Also, the distances between the adult tree and seedling communities were greater locations at locations with Melia, except for Location 1, which may indicate some effect of the presence of Melia trees on successive communities. NMDS analysis at the level of individual plots shows that plots with Melia have more similar composition (lesser spread in the ordination space) than plots without Melia (Fig. 4). The multivariate GLM indicated a significant difference between assemblages with and without Melia (Wald $\chi^2 = 8.54$, P = 0.02). In addition, it pointed to a difference in the composition of the assemblages in terms of plant stages, specifically adults vs seedlings (Wald $\chi^2 = 9.03$, P = 0.01); this may indicate the entering of new species as seedlings (Appendix Table 4) and no permanence of

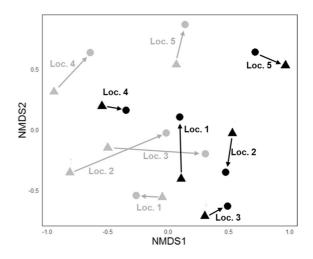
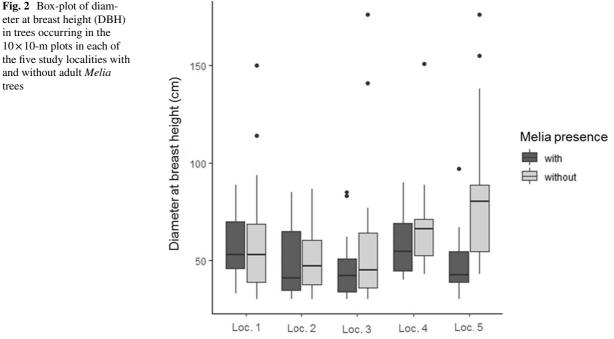
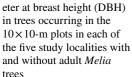


Fig. 3 Non-metric multidimensional scaling of adult trees (triangles) and seedling (circles) communities at the five localities surveyed in the study. Arrows point from the adult tree community to the seedling community at the same locality. Grey symbols: with adult Melia, black symbols: without adult Melia trees. Site numbers are labelled on the figure

adult plants. Therefore, the plant species dynamics point to change in the composition. However, that change does not seem to be related to Melia presence, because the interaction of both effects was not significant (Wald $\chi^2 = 3.49, P = 0.68$).





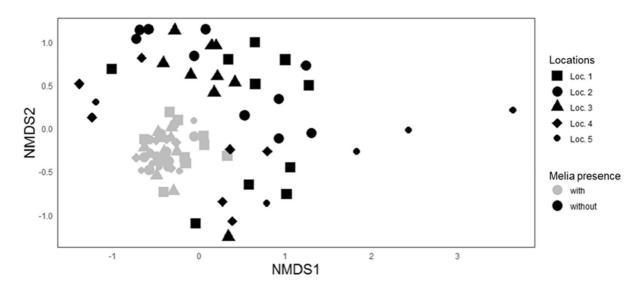


Fig. 4 Non-metric multidimensional scalingof adult trees per plot at the five localities (distinguished using different symbols) with and without *Melia* trees surveyed in the study

Discussion

Plots where *Melia* trees were present have lower tree species richness, diversity and lower DBH compared to those where they were absent. The differences may indicate that Melia can impact on both biodiversity and vegetation structure, under the assumption that the pre-invasion state of the invaded and uninvaded localities was comparable. It is also notable that the richness of seedlings was lower than adult tree richness in plots where adult Melia trees were present, so the invasion had already been in place for a long time. Of course, as this is not a longitudinal study considering the progression of the tree community over many years, it could be argued that this was the case even before Melia invasion and that these differences do not capture Melia impacts but pre-existing vegetation differences. Indeed, besides woodlands (Mavimbela et al. 2018), Melia is known to invade savanna vegetation (Henderson and Musil 1984; Henderson 2007), which is naturally less diverse in trees in the study region, and is characterized by smaller trees compared to woodlands (Mucina and Rutherford 2006), and in the absence of fire, any savanna can become a woodland. The dynamics of biomes and subordinate vegetation types in Durban are such that their identification is not always easy. In particular, the identification of past vegetation following changes in fire regime and grazing, which would certainly occur following urbanization, is not as obvious as to always impact site selection (see Mucina and Rutherford 2006). Therefore, our localities could potentially include a diversity of vegetation types, meaning some of our localities could have fairly recently been dominated by grassy or partly grassy vegetation. The NMDS on the assemblages of adult trees showed significant reduction of diversity of the invaded communities (all plots similar to each other, Fig. 4). In Fig. 3, there is also a tendency of positioning of the localities with and without Melia right and left, respectively. Moreover, the distances between seedling and adult tree assemblages distances (arrows) are large at most localities with Melia trees. Those may indicate that the presence of *Melia* may have interfered with the past vegetation and with the destiny of the next one (Fig. 3). Also, the multivariate analysis shows a significant difference to adult vs seedling assemblages and among Melia-infested localities (Fig. 3), but no relation to interaction. However, there are many factors that drive invasions, climate, soil types, etc. The behaviour of frugivorous birds will also determine the distribution of seedlings, and micro-climates can impact germination and growth, etc. The findings require cautious interpretation, as it can also be argued that these invaded sites were possibly speciesdepauperate before the invasions.

While we did not directly quantify the impact of other invasive plants, there is little doubt that these, too, put further pressure on the native trees present at our localities, both in terms of diversity and growth. Of the trees recorded at our localities, only Morus alba was, at one locality, abundant on a scale comparable to our target species. However, Solanum mauritianum and Litsea glutinosa are major landscape transformers in our study region and elsewhere (Witkowski and Garner 2008; Atkinson et al. 2014; Mavimblea et al. 2018). Among shrub species, both Chromolaena odorata and Lantana camara are major problem species in Durban, even though more common in grasslands, which they subsequently convert into novel woody assemblages (Witkowski and Wilson 2001; Sharma et al. 2005). Lantana camara and C. odorata easily invade forest and woodland gaps and edges, and also savanna and grasslands, etc. Although present at our localities, and not quantified, their impact was unlikely to be comparable to that of Melia, because of overall lower cover. However, these species can have a dramatic impact on seedling recruitment because of their allelopathic nature. Another factor not considered here is the possibility of episodic recruitment, common among trees (Wiegand et al. 2004) and likely to bias any one-off assessment of seedling community composition. Melia is a fleshy-fruited tree with mass blooming and fruiting virtually every year, and dispersal is unlikely to be a limiting factor (Voigt et al. 2011). Therefore, we do not believe that episodic recruitment would have biased our assessment of Melia seedling abundance, but we do acknowledge that it may have biased our results as far as seedlings of other tree species, indigenous and alien, are concerned.

The diverse trajectories of the tree assemblages, from the current state represented by adult trees to a potential state as inferred from seedling representation (Fig. 3), suggest that the impacts of the Melia invasion on tree community structure are driven by specific local factors such as the indigenous tree species that dominate or the presence of dispersal agents (Voigt et al. 2011). Direct human exploitation of certain tree species for construction or medicinal purposes (see Boon 2010), or even differential removal of alien plants specifically in order to control them, cannot be discounted. The control of invasive alien trees in Durban is affected by several branches of the eThekwini Municipality, as well as by local communities, in ways that cannot be easily tracked or summarized but involve both chemical and physical measures. Although the actual tree communities observed at these localities in a decade or two will no doubt differ from the current seedling communities because of competition, exploitation, etc., the multivariate analysis indicates that these potential communities fall within the range of currently observed ones in terms of species composition and representation. In addition, it confirms the expectation that recentlyinvaded localities (seedlings only) are changing richness rapidly, and there may be further implications. Plots dominated by indigenous trees are characterized by high species diversity, and these diverse species presumably use different resources, thus resulting in fairly high turnover for any given area. Comparatively, localities that have been invaded for a long period of time may have, in fact, settled in terms of species representation to some extent, reaching a novel stable state. Such stable states may incur no further species loss, and cover variations in the dominant invasive species may fluctuate within moderately broad limits. This type of temporal pattern has been documented in several cases in woody plant invasions elsewhere, both in urban and protected areas (Jäger et al. 2009; Nowak et al. 2016). Nevertheless, whether this is the case with Melia at our study localities remains to be seen.

Worldwide, the impacts of dominant invasive plants on indigenous biodiversity have been documented in numerous cases, and the results have been summarized (Powell et al. 2011), indicating that these effects are mostly detrimental, although with numerous exceptions, and dependent on spatial scale. Although Melia certainly has detrimental effects on ecosystem functioning (see the Introduction) and on tree community diversity and size distribution (see our results), one should not overstate its overall impact on biodiversity. The fleshy fruit produced by this alien tree attracts multiple indigenous birds (Voigt et al. 2011), and alien fleshy fruit in our study area has been shown elsewhere to host diverse insect assemblages (Padayachi et al. 2014). Furthermore, the fair number of other trees that can coexist with Melia, and its propensity to support other plants such as mistletoe (Gairola et al. 2013), indicate that, although impoverished, Melia-infested communities are not absolute biodiversity gaps. On the other hand, it can be argued that the seedlings of adult trees in invaded ranges are unlikely to survive, and in the long run, it is likely that diversity will be reduced even further. Whether the impacts of the *Melia* invasion will not increase over time remains to be seen, though; it is possible that the diversity of co-habiting indigenous trees was yet to decrease at our localities. It would also be interesting to determine whether *Melia* can facilitate the invasion of other alien plants, thus having a part in invasional meltdown processes (Simberloff and Von Holle 1999).

The Melia invasion will undoubtedly have profound long-term impacts on the community structure and dynamics of woodland and savanna communities in South Africa. Its sheer scale across large portions of southern Africa – mainly, but not only in its eastern half – means that control throughout its range is not possible (see Marais et al. 2004; Richardson and van Wilgen 2004). In such a situation, the best possible course of action is better understanding its relationships and impacts, ideally through removal experiments and long-term studies monitoring a broad range of plant and animal groups. Biological control of invasive plants has gained enormous momentum in South Africa (Hill et al. 2020). It is generally accepted as the most cost-effective control method and could be considered possibly the best long-term control measure. In urban areas, where human effort levels can be maintained at a relatively high level, controlling the species may be locally possible by employing herbicides as basal bark treatment and the physical removal of stumps (Bromilow 2001). If resources were made available, efforts could also be made to source host-specific and damaging biocontrol agents that would reduce the costs of other management interventions. Utilization for diverse reasons (medicinal and ritual; Dharani et al. 2010; Sharma and Paul 2013) may be brought in to strengthen such efforts, although the chances are that, even in densely populated areas, the supply will vastly exceed any demand for Melia products. Outside cities, control will probably only be feasible over relatively small areas. In this context, new foci of invasion and areas of high biodiversity, and specifically areas high in those biodiversity components worst affected by Melia invasion, need to be prioritized once such impacts are understood.

In the present study, there is a limitation in our sampling strategy that deserves mention and suggests caution in the interpretation of our results. In our future study, where possible, we will use belted transects across a locality, where a several metres wide transect could give a better idea of species associated with *Melia* across the landscape.

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Credit Authorship Contribution Statement AB, SG and YG joinlty carried out the conceptualization, survey, data collection, analysis and writing the manuscript, and PRMSF helped in data analysis and revising the final draft of the manuscript.

Declarations

Declaration of Conflict of Interest The authors declare that they have no conflict of interests.

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