



Biological and Microbial Control

An Assessment of the Potential Economic Impacts of the Invasive Polyphagous Shot Hole Borer (Coleoptera: Curculionidae) in South Africa

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Abstract

Studies addressing the economic impacts of invasive alien species are biased towards ex-post assessments of the costs and benefits of control options, but ex-ante assessments are also required to deal with potentially damaging invaders. The polyphagous shot hole borer *Euwallacea fornicatus* (Coleoptera: Curculionidae) is a recent and potentially damaging introduction to South Africa. We assessed the potential impact of this beetle by working across economic and biological disciplines and developing a simulation model that included dynamic mutualistic relations between the beetle and its symbiotic fungus. We modeled the potential growth in beetle populations and their effect on the net present cost of damage to natural forests, urban trees, commercial forestry, and the avocado industry over 10 yr. We modeled high, baseline, and low scenarios using discount rates of 8, 6, and 4%, and a plausible range of costs and mortality rates. Models predicted steady growth in the beetle and fungus populations, leading to average declines in tree populations of between 3.5 and 15.5% over 10 yr. The predicted net present cost was 18.45 billion international dollars (Int. \$), or about 0.66% of the country's GDP for our baseline scenario (\$2.7 billion to \$164 billion for low and high scenarios). Most of the costs are for the removal of urban trees that die as a result of the beetle and its fungal symbiont, as has been found in other regions. We conclude that an ex-ante economic assessment system dynamics model can be useful for informing national strategies on invasive alien species management.

Key words: Ambrosia beetle, biological invasion, economic assessment, *Euwallacea fornicatus*, ex-ante decision support

Invasive alien species can have substantial economic impacts, and ecologists are learning that early proactive management often offers the best way to limit negative impacts, reduce risks, and save money (Wilson et al. 2017). Given that the number of potentially damaging species is increasing, it is also necessary to prioritize interventions, and such prioritization exercises should be based on predictions of potential impact. The potential extent and scale of impacts, including economic consequences, are unknown during the early stages of invasion, and ex-post economic assessments (assessments

based on actual impacts) are not feasible. It is thus necessary to provide ex-ante assessments (based on forecasts) to inform prioritization and policy development.

A recent addition to the list of invasive species that cause major impacts in South Africa is the polyphagous shot hole borer, *Euwallacea fornicatus* (Eichhoff) (Coleoptera: Curculionidae) and its fungal symbiont, *Fusarium euwallaceae* S. Freeman, Z. Mendel, T. Aoki et O'Donnell (Hypocreales: Nectriaceae). This ambrosia beetle, native to South East Asia (Stouthamer et al. 2017), has become

invasive in California, Hawaii, and Israel (Rabaglia et al. 2006, Mendel et al. 2012, Rugman-Jones et al. 2020). In South Africa, it was first detected in 2012 (Stouthamer et al. 2017), and was later found to have been established on London plane trees (*Platanus × acerifolia*) (Aiton) Willd. (Proteales: Platanaceae) (Paap et al. 2018). Since then, *E. fornicatus* has been found in eight of South Africa's nine provinces, with some infestations separated by more than 1,000 km (Fig. 1), making it the largest current outbreak of this invasive pest globally.

E. fornicatus constructs galleries in susceptible host trees and inoculates these with its fungal symbionts (including the pathogen *F. euwallaceae*) which serve as a primary food source for *E. fornicatus* (Eskalen et al. 2013, Freeman et al. 2013, O'Donnell et al. 2015). Once the insect locates a suitable host tree, successful colonization can lead to *Fusarium* dieback, a disease that can be fatal to trees at high levels of injury. As the beetles do not feed directly on the host, any tree species in which the mutualistic fungus can proliferate may become a potential host. In South Africa, the fungus has been established on more than 100 plant species, many of which die as a result (van Rooyen et al. 2021). The hosts include major crops such as avocado (genus *Persia* Mill. [Laurales: Lauraceae]), lemon and orange (both genus *Citrus* L. [Sapindales: Rutaceae]), fig (genus *Ficus* L. [Rosales: Moraceae]), macadamia (genus *Macadamia* F. Muell. [Proteales: Proteaceae]), pecan nut (genus *Carya* Nutt. [Fagales: Juglandaceae]), peach (genus *Prunus* L. [Rosales: Rosaceae]), and guava (genus *Psidium* L. [Myrtales: Myrtaceae]) trees, important plantation forestry trees, and large numbers of native and urban trees, with urban trees being especially vulnerable (Eskalen et al. 2013).

The international literature shows that *E. fornicatus* is a particularly vigorous invader. Actual data on impacts and damage are scarce. *E. fornicatus* is known to have caused damage to thousands of trees in southern California (Coleman et al. 2019), where ornamental trees in cities and towns are most heavily impacted (California Forest Pest Council 2015). However, while the impacts of these beetles are evident, they remain largely unquantified.

Given that the invasion in South Africa is at an early stage, we know very little about both its current and potential future spread and impact. Although *E. fornicatus* is native to equatorial climates, it has already become established in both temperate (California and Israel) and tropical (Hawaii) climates. South Africa's climate is therefore likely to be suitable for the establishment of this species over an extensive area. Further, the broad range of plant species in which the beetle and fungus can establish (Gomez et al. 2019) increases the chances of a suitable host being encountered, thus increasing the chances of successful establishment and spread (van Rooyen et al. 2021).

There is a strong need to develop economic assessment tools in support of decision-making ex-ante. Ex-post economic assessments are not an option in the case of potentially high-impact invaders that are at an early stage of invasion. Ex-ante approaches must include a preliminary estimation of damages while accounting for dynamics and uncertainty. Developing a robust understanding of the spread and impact of a high-risk species such as *E. fornicatus* will require inputs from both biologists and economists. The lack of data needed for economic analysis, and the infrequency of collaboration between invasion scientists and economists, seriously limits our ability to understand and deal with biological invasions. This

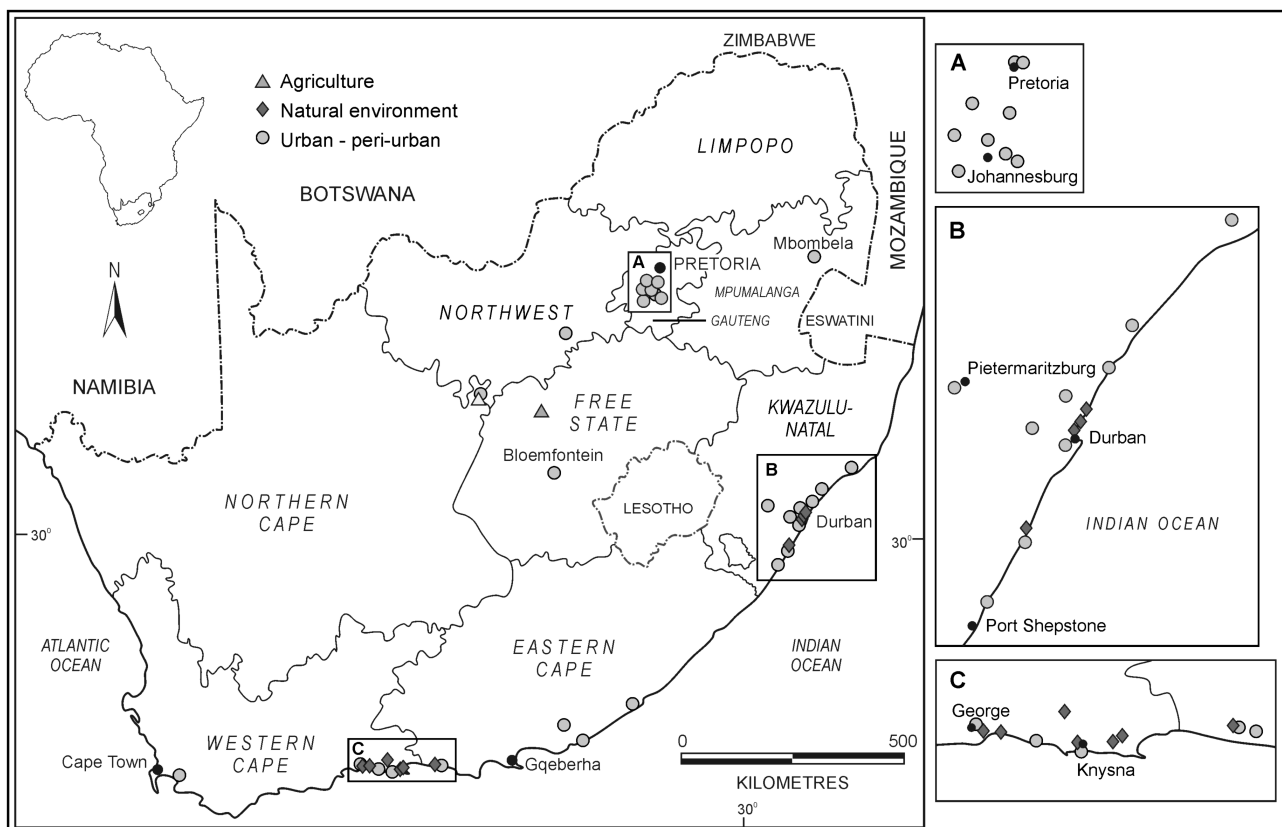


Fig. 1. Locations in South Africa where the presence of the polyphagous shot hole borer, *Euwallacea fornicatus* S. Freeman, Z. Mendel, T. Aoki et O'Donnell, and its fungal symbiont *Fusarium euwallaceae* (Eichhoff) have been confirmed (current 29 October 2021).

issue was included in the top 20 issues pertaining to invasive species management in Europe (Caffrey et al. 2014). Expert opinion developed through interdisciplinary collaboration can reduce uncertainty in economic and biological parameters by defining robust ranges for model parameters (Touza et al. 2007).

In this study, we combined standard economic assessment approaches with expert opinion from biologists to develop a simulation model for a new and rapidly expanding invasive alien species. *E. formicatus* is characterized by potentially high economic impacts where there is little information on population dynamics, and uncertainty about spread, impacts, and the efficacy of mitigation options. Our analysis provides a plausible estimate of the unmitigated spread of *E. formicatus* in South Africa, and its potential economic impacts. The benefit of such an approach is that it provides evidence to support the development of strategies, policies, and legislation for dealing with the problem.

Materials and Methods

Modeling Approach

We developed a system dynamics model to simulate the population dynamics of *E. formicatus* and its symbiotic fungus, and how that would affect host tree mortality over time (Fig. 2). The model is based on Lotka-Volterra equations that mimic the positive and negative feedbacks between the beetle population, the fungus population, and the mortality of host trees (Fig. 3). The population size and mortality rate estimates then feed into stock flow models that estimate the number of trees affected. Separate sets of equations and stock flows were developed for avocados, black wattles, natural forest trees, and urban trees (Supp. Appendix S1 [online only]). The system dynamics model was developed in Vensim DSS version 6.4b (Ventana Systems Inc. 2015). The Vensim modeling package is frequently used for these types of models (Sterman 2000). The Euler method (Euler 1741) for numerical integration of ordinary differential equations was used to determine the evolution of the system of equations over time (Fortunato 2010). The outputs (number of trees affected) were then used in combination with estimates of the monetary value of costs to estimate the net present value of projected costs per year between 2020 and 2030.

Selection of Tree Species at Risk

Natural forests, urban trees, commercial forestry, and agricultural tree crops are all under threat from beetles in the genus *Euvallacea* Hopkins, 1915 (Coleoptera: Curculionidae) (O'Donnell et al. 2016, Lynn et al. 2020). We had to focus our study only on those species

where basic information was available, or where we could draw on information from closely-related tree species from other parts of the world. These were commercial tree crops, plantation trees, trees in natural forests, and urban trees.

For commercial tree crops, the avocado (*Persea americana* Mill. [Laurales: Lauraceae]) is the primary species affected by *E. formicatus*. While other trees are known to be affected by *E. formicatus* in other countries, they were excluded from our analysis due to a lack of any information in a South African context. For commercial forestry, only black wattle (*Acacia mearnsii* De Wild. [Fabales: Fabaceae]) is currently known to be a reproductive host for *E. formicatus* in South Africa. Van Rooyen et al. (2021) identified 19 indigenous South African tree species that were able to maintain breeding populations of *E. formicatus*. Studies on monitoring plots in natural forests in the Western Cape found that 9% of 2195 individual native trees were infested by *E. formicatus*, almost all of which showed signs that they would suffer dieback and possible death (E. van Rooyen, G. Townsend, unpublished data). Visual surveys of urban trees in Johannesburg (Gauteng Province), Knysna, George and Somerset West (Western Cape Province) revealed that nearly all individual *Quercus robur* L. (Fagales: Fagaceae) (English oak), *Acer negundo* L. (Sapindales: Sapindaceae) (box elder) and other maples (*Acer* L. [Sapindales: Sapindaceae] species) will die when infested by *E. formicatus*, as well as about half of London plane trees (*Platanus × acerifolia*). About 50% of the street trees sampled in the northern suburbs of Johannesburg were London planes (*Platanus × acerifolia*), 40% were oaks (*Quercus* L. [Fagales: Fagaceae] species) and < 5% were maples (*Acer* species) (M.J. Byrne, personal communication). In Somerset West and Stellenbosch, the dominant street trees are among the species most highly impacted by *E. formicatus*, including English oak, *Acer* species, London plane, and *Populus* L. (Malpighiales: Salicaceae) species (poplar) (F. Roets, unpublished data).

Tree Mortality Rates

Some information on infection rates for avocados is available from Israel and California, where infested orchards showed high branch dieback and mortality (Eskalen et al. 2012, Freeman et al. 2013), with yield losses of up to 100% reported in some instances (Eskalen 2012). Damage depended on the susceptibility of the specific variety and on the method of control. *Hass* is one of the most susceptible varieties in Israel (Eskalen et al. 2012, Mendel et al. 2017), and is also one of the most widely planted varieties in South Africa (van Zyl & Ferreira 1995). More recent observations suggest that avocados may not be as susceptible as originally

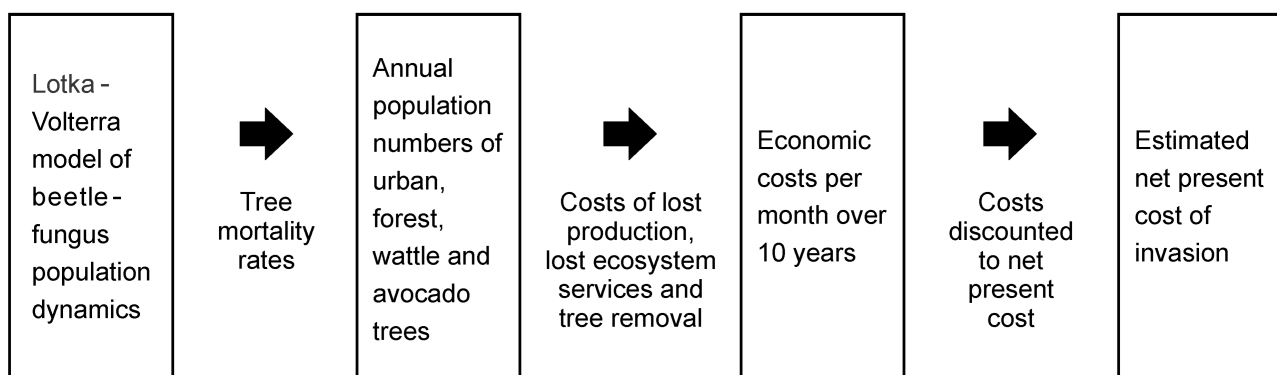


Fig. 2. Basic structure of a system dynamics model to estimate the net present cost of invasion by the polyphagous shot hole borer in South Africa.

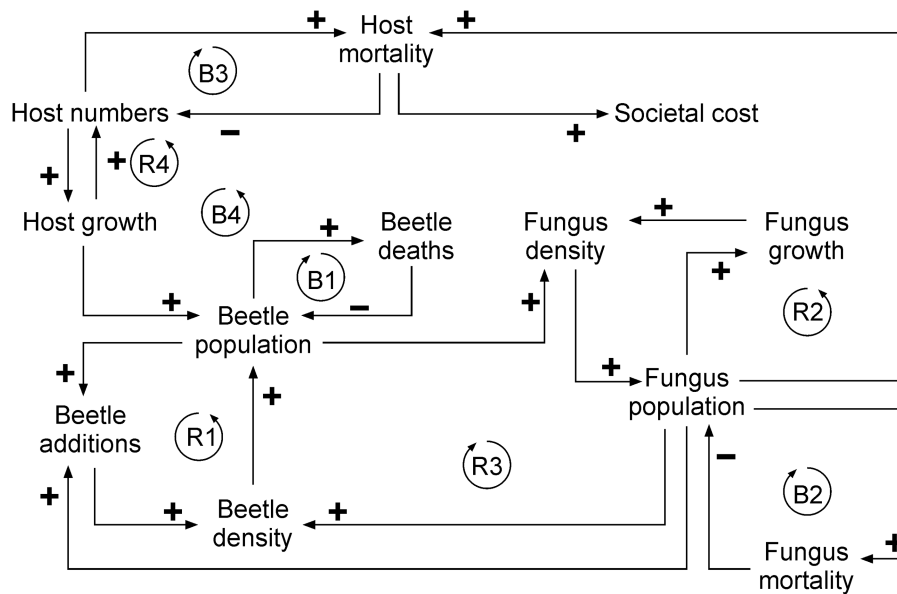


Fig. 3. Causal loop diagram showing the main feedback loops in the Lotka-Volterra model. Feedback loops are either reinforcing (R, leading to exponential growth or decline) or balancing (B, where the loop converges on a goal or steady-state).

anticipated, and that damage could be mitigated through management (Mendel et al. 2017). Coleman et al. (2019) present data for 128 avocado trees in a Californian grove. While >90% of trees were infested, only low levels of injury were observed with no resulting mortality, and additional surveys are required to confirm potential impacts (Coleman et al. 2019). In light of the conflicting reports and uncertainty regarding the impact of *E. fornicatus* on commercially-grown avocado in South Africa, we assumed the loss in production to be in the range of 2–10%, with a baseline of 6% over 10 yr.

For *Acacia mearnsii* in South Africa, estimates were made from information on other Australian *Acacia* Mill. (Fabalea: Fabaceae) species elsewhere. Coleman et al. (2019) assessed 116 *A. mangium* Mill. (Fabales: Fabaceae) Willd. trees across six sites in Vietnam and found <2% mortality, noting that short growing rotations (approximately 7 yr) could limit damage. Thu et al. (2021) reported mortality rates of 2–5% for *Acacia auriculiformis* Cunn. Ex. Benth (Fabales: Fabaceae), *A. mangium* and *Acacia* hybrids. The growing rotation for *A. mearnsii* in South Africa varies from 8–12 yr (Chan et al. 2015). Based on Thu et al.'s data, we assumed the loss in wattle production to be in the range of 2–5%, with a baseline of 3.5% over 10 yr.

In the case of natural forests, the only published assessment of impact comes from Coleman et al. (2019), who present combined mortality data for ornamental ($n = 889$) and native ($n = 1\,594$) individual trees from 38 species in California and Asia. Overall, the mortality rate was ca. 6%, but a further 18% of trees showed moderate to severe dieback, indicating that mortality rates could increase over time. Based on the unpublished data from native forest plots in South Africa, and the reports from Coleman et al. (2019), we assumed a lower limit of 6% mortality, an upper limit of 11%, with a baseline of 8.5% over 10 yr.

For urban trees, the Californian data for ornamental and native forest trees (Coleman et al. 2019), and preliminary observations made from *E. fornicatus*-infested urban areas of South Africa, suggest that urban tree losses will be in the range of 6–25%, with a baseline of 15.5% over 10 yr.

Mortality estimates were used to scale up expected losses for urban and natural forest trees by estimating the number of trees in the country. The number of urban trees in South Africa was obtained from three urban centers (Johannesburg: Schäffler et al. 2013; Cape Town and Durban: Treepedia 2020), and scaled up using the World Bank data portal for urban coverage in South Africa (CIESIN 2013). Total number of trees in natural forests were estimated from the extent of forest (Mongabay 2011) multiplied by estimated number of trees per hectare from NCT Forestry Co-Operative Ltd (2014). For avocados and wattles, the mortality estimates were used to estimate losses in production, based on estimates of projected production over 10 yr (see below).

Estimation of Costs

The monetary value of impacts caused by *E. fornicatus* can be divided into private costs (those borne by individuals) and external costs (those borne by society at large). The losses for the commercial forestry and agricultural tree crops would be private costs that come about from losses in production. In the case of natural forests and urban trees, the loss of ecosystem services associated with these trees would be nonmarket values, i.e., external costs (Holmes et al. 2009). Private costs would also come about where dead trees have to be removed. By far the largest component of these removal costs would come from removing urban trees that were included in the model. Costs of removal for commercial forestry and agricultural tree crops were not available and have not been included in the model. Monetary values are expressed in international dollars (Int. \$) in this study, i.e., a hypothetical (average or world) unit where the national currency is expressed in U.S. dollars, adjusted by the global purchasing power across all countries (Eurostat and OECD 2007).

The gross production value for avocados (i.e., the mass produced multiplied by the producer price per ton) has grown over time (Department of Agriculture, Forestry and Fisheries' Agricultural Statistics, DAFF 2020). The most recently reported value was Int. \$127.79 million for the year 2017/2018 (Supp. Appendix S2 [online only]). Based on the rate of growth in production, we projected that

the price would increase from Int. \$21 771/t in 2020 to Int. \$31 188/t in 2030.

As with avocados, the gross production value for black wattle has grown over time (Supp. Appendix S2 [online only]). The volumes of roundwood sales for 2002–2019 were obtained from Oberholzer and Godsmark (2020), and prices of timber were collected from NCT Co-operative Limited (Craig Norris, personal communication). Bark prices were obtained from the Department of Agriculture, Forestry and Fisheries' Agricultural Statistics (DAFF 2020). Based on the rate of growth, we projected that the combined roundwood and bark price would grow from Int. \$1,739/t in 2020 to Int. \$2,491/t in 2030.

The ecosystem services provided by natural forests include provisioning, regulating, supporting, and cultural services, and the external costs of losing natural forests include carbon values and other ecosystem services (Turpie et al. 2017). As local studies on natural forests were not available, we consulted Brenner et al. (2010) and De Groot et al. (2012, 2013) for monetary values and transferred these to the South African context by adjusting them following guidelines on the application of the benefit-transfer method (Saplaco and Francisco 1993). These included adjustments for exchange rates, inflation, and purchasing power parity (see Supp. Appendix S3 [online only] for further details). The adjusted total economic values ranged from Int. \$2,111.23 to Int. \$6,642.87 per hectare, and a mean value of Int. \$4,380 per hectare was used for the baseline estimate.

The ecosystem services provided by urban trees include atmospheric carbon dioxide reduction, air quality improvement, storm water runoff reductions, as well as aesthetic, property value, social, economic, and other benefits. As in the case of natural forests, local studies were not available, and we consulted studies by McPherson (2003), Peper et al. (2007) and Soares et al. (2011) to establish values, using the benefit transfer method as above. Economic values for *Platanus × acerifolia* (London plane), *Fraxinus velutina* Torr. (Lamiales: Oleaceae) (Modesto ash) and *Liquidambar formosana* Hance (Saxifragales: Altingiaceae) (Chinese sweetgum) were taken from data in McPherson (2003) for urban trees in Modesto, California. Peper et al. (2007) provided economic values for the London plane, Chinese sweetgum [which we used as a proxy for American sweetgum (*Liquidambar styraciflua* L. (Saxifragales: Altingiaceae))—a host species of *E. fornicatus* in South Africa], *Quercus palustris* Münchh. (Fagales: Fagaceae) (pin oak), *Q. rubra* L. (Fagales: Fagaceae) (northern red

oak), and a variety of maple (*Acer* species), which are averaged and used as a proxy for *Acer palmatum* Thunberg (Sapindales: Sapindaceae) (Japanese maple) which is a host species of *E. fornicatus* in South Africa. The minimum economic value of an urban tree is estimated at Int. \$8.22 for Chinese sweetgum, as adjusted from McPherson (2003). The maximum economic value of an urban tree is Int. \$44.04 for the London plane as adjusted from Peper et al. (2007). The mean of Int. \$25.07 per urban tree was used as a baseline.

Estimation of Impact

We used the above estimates as input variables into our system dynamics model. Internal validation was done by the modeler and external validation in a series of interdisciplinary workshops involving the authors and consultation with many people (see the Supp. Material [online only] for a full list of validation techniques employed). For each type of tree we estimated a low, a baseline, and a high value of the net present cost of invasion over the next 10 yr. The low, baseline, and high costs were estimated using discount rates of 8, 6, and 4%, and low, baseline, and high costs respectively (Table 1). Estimates of mortality rates were obtained from the assumptions of plausible mortality rates over 10 yr (see above), adjusted to a mortality rate per month. The three scenarios, therefore, represent best and worst-case estimates, with the baseline being the most plausible outcome.

Results

Effects on Tree Dieback

The model predicted a steady increase in the *E. fornicatus* population over the next 10 yr, with a corresponding increase in the spread of the *Fusarium* fungus (Fig. 4, panels A1 and A2). We estimated that there are 255 million urban trees in South Africa. Under the baseline scenario, urban trees are expected to decline by around 65 million trees over the next 10 yr (Fig. 4, panel B1). Forest trees are expected to decline by around 50,000 hectares (Fig. 4, panel B2), and wattles by roughly 140,000 trees over the next 10 yr (Fig. 4, panel B3). Avocado trees are expected to increase initially as a result of the ongoing establishment of new orchards, but will decline by around 30,000 trees at the end of the simulation period (Fig. 4, panel B4).

Table 1. Values of parameters used in three scenarios to model the cost of lost ecosystem services, and clearing of dead trees following attack by the polyphagous shot hole borer in South Africa

Scenario	Type of tree	Discount rate (%)	Mortality rate (% per month)	Clearing cost (Int. \$ per tree)	Loss of ecosystem services (Int. \$ per tree)	Value of production 2020 (Int. \$ per year)	Value of production 2030 (Int. \$ per year)
Low	Urban	8	0.9	281.38	8.22	0	0
	Forest	8	0.9	0	1.41	0	0
	Wattle	8	0.45	0	0	1,739	2,491
	Avocado	8	2	0	0	21,771	31,188
Baseline	Urban	6	2.45	656.55	25.07	0	0
	Forest	6	1.3	0	2.92	0	0
	Wattle	6	0.65	0	0	1,739	2,491
	Avocado	6	2.65	0	0	21,771	31,188
High	Urban	4	4.2	3283	44.04	0	0
	Forest	4	1.69	0	4.43	0	0
	Wattle	4	0.88	0	0	1,739	2,491
	Avocado	4	3.3	0	0	21,771	31,188

Loss of production was based on ongoing mortality against a background of rising production values between 2020 and 2030.

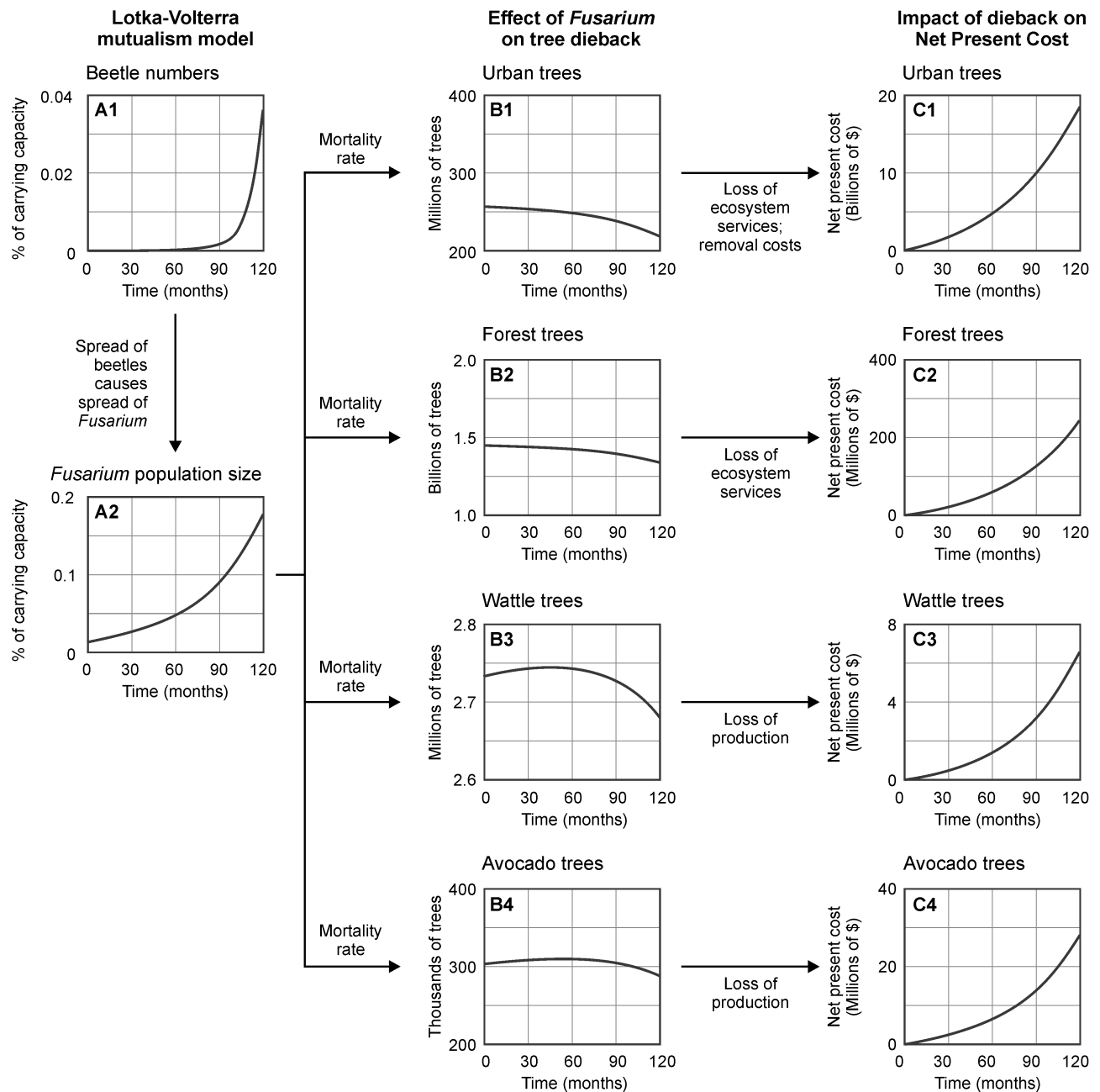


Fig. 4. Model outputs (baseline scenario values) for four types of trees predicted to be affected by the polyphagous shot hole borer in South Africa over the next 10 yr. Column A shows the outputs of a Lotka-Volterra model of beetle and fungus populations. Column B shows the projected number of trees over the next 10 yr, assuming that no control takes place. Column C shows the increase in costs resulting from ongoing tree mortality.

Estimated Net Present Cost

Net present costs will accumulate over time as tree mortality progresses (Fig. 4, panels C1–C4). The estimated net present cost of the potential spread of *E. fornicatus* and its associated fungus in South Africa is Int. \$18.45 billion (baseline value, 2019 prices, Table 2). The removal cost of dead urban trees dominates the estimated unmitigated total social cost values, which are estimated at Int. \$17.51 billion (baseline value). The cost of the invasion in terms of lost production (wattle and avocados) and the loss of ecosystem services (natural forests and urban trees) combined is estimated at a further Int. \$942.7 million (baseline value). For urban trees, the social cost of an *E. fornicatus* infestation is projected to be Int. \$18.18 billion; for primary forests, the social cost of *E. fornicatus* infestation is estimated at Int. \$238 million; for wattle the cost of *E.*

fornicatus infestation on black wattle is Int. \$6.5 million; and for avocados, the cost of *E. fornicatus* infestation on production is \$28 million (baseline value). The high and low scenarios suggest that the estimated total social cost associated with a loss of urban trees due to *E. fornicatus* infestations could be anywhere between Int. \$2.7 billion and Int. \$164 billion.

Discussion

Relative Magnitude of Predicted Impacts

Our assessment of the baseline unmitigated social cost of *E. fornicatus* invasion in South Africa predicts substantial economic losses to the economy and society. Other studies have calculated economic losses due to ambrosia beetle invasions, but these have been

Table 2. Estimated net present costs (millions of 2019 International \$) of an invasion by the polyphagous shot hole borer for three scenarios in South Africa

Type of trees	Scenario		
	Low (8% discount rate)	Baseline (6% discount rate)	High (4% discount rate)
Urban trees	2,630	18,180	163,550
Forest trees	71	238	529
Wattle trees	4	6.5	10
Avocado trees	19	28	39
Total	2,724	18,453	164,128

limited to the timber industry in Canada (Orbay et al. 1994) and in the Southeastern United States (Susaeta et al. 2016), or to forest lands in the United States (Adams et al. 2020). In Florida, the redbay ambrosia beetle (*Xyleborus glabratus*, Eichhoff 1877 [Coleoptera: Curculionidae]), along with its fungal symbiont, the laurel wilt pathogen, caused the mortality of 7,000 avocado trees, or 1% of production area, between 2011 and 2015 (Mosquera et al. 2015). Evans et al. (2010) estimated that the economic losses to the avocado industry in Florida, in terms of lost sales, property damage, and increased management costs, could equate to \$356 million under a “do nothing” scenario. Differences in model specifications and selection of economic impacts in these studies make direct comparisons with our results difficult other than confirming that the economic costs of ambrosia-type beetle infestations could be substantial for certain sectors.

National-scale economic assessments on the possible economic impacts of *E. formicatus* invasions are not readily available to inform comparisons between countries. What is useful is to compare our results to the size of the South African economy as a whole. In 2019 South Africa’s gross domestic product (GDP) was \$351 billion (current prices) (World Bank 2020). Using the IMF (2021) economic growth forecasts up to 2024 and assuming 2% growth per year after that until 2030 as well as a constant exchange rate, the net present value of South Africa’s economy at a baseline discount rate of 6% is calculated at \$2.8 trillion. The unmitigated baseline social cost of \$18.45 billion in the case of an *E. formicatus* invasion in South Africa would be in the order of 0.66% of the country’s GDP, or approximately \$35 per person per year in South Africa. These numbers are incomplete estimates; broader indirect and induced economic impacts are excluded and estimates are, therefore, conservative.

Although the expected costs of an *E. formicatus* invasion on commercial black wattle and avocado are meaningful in the context of the overall value of these sectors, the striking finding arising out of our analysis is that the loss of urban trees would be by far the largest cost component at a national level. This finding emphasizes the need for an ex-ante economic assessment to inform the prioritization of resources at the early stages of a potentially high-impact invasive alien species. Most of the costs in our model are for the removal of impacted urban trees, but they also include a loss in ecosystem services provided by urban trees. The relatively high costs of impacted urban trees due to beetle invasions have also been documented elsewhere (Aukema et al. 2011). One scenario proposed by McPherson et al. (2017) generated a projected loss of 11.6 million trees due to an invasive shot hole borer (*Euwallacea* sp.) in Southern Californian cities at the cost of removal and replacement of \$15.9 billion, and with a value of ecosystem services foregone over 10 yr of \$616.6 million. Kovacs et al. (2010) estimated that the discounted cost of

treatment, removal, and replacement of 17 million urban trees in case of an invasion of *Agrilus planipennis* (emerald ash borer) in the United States would amount to \$10.76 billion (discounted 2009 values), a value that was updated to \$12.5 billion in a later baseline scenario; these costs do not include estimates of ecosystem services (Kovacs et al. 2011). The discounted costs per tree in these studies in the United States are higher, but of the same order of magnitude as our estimates (63.75 million urban trees at a discounted social cost of \$26.7 billion). The higher values in the United States studies can be explained by several factors such as the inclusion of replacement costs, a differentiation in the costs of removal across tree sizes, and the possible difference in the costs of urban tree management in the United States compared to South Africa.

Options for Management

Mitigating the future impact of *E. formicatus* in South Africa will be no easy task. Given how widespread *E. formicatus* is, eradication is impossible and management will have to focus on reducing further spread. Female beetles have a limited flying range (500 m to 2 km), but this can be aided by the wind to a spread rate of up to 20 km per year (Leathers 2015, Owens et al. 2019). In Somerset West in the Western Cape, *E. formicatus* spread at least 3 km from the putative point of introduction in only three months, and in the opposite direction to the prevailing winds (F. Roets personal observation). Natural spread can therefore be significant, but the long-distance spread of *E. formicatus* is enabled by the ease of movement of infested wood and planting material (Grousset et al. 2020). As a developing country, a large proportion of households in South Africa are heavily dependent on wood for their energy needs (Guild and Shackleton 2018); this presents a probable pathway for long-distance spread. Recreational barbecue fires may arguably present an even greater long-distance dispersal risk, as firewood is often transported over hundreds of kilometers, even into pristine natural environments. The trade in infested nursery material may present another significant, although unproven, long-distance dispersal pathway for *E. formicatus* in South Africa. A first step, and likely the most economical of the potential mitigation factors in curbing long-distance spread of *E. formicatus*, should be to restrict the free movement of potentially infested planting material, wood, and wood products.

Management options once *E. formicatus* has been established are fairly limited. Although there is currently no known pheromone for *E. formicatus*, Quercivorol (an aggregation pheromone identified for the oak-killing ambrosia beetle *Platypus quercivorus* Murayama, 1925 [Coleoptera: Curculionidae]) has shown potential as an attractant. It is suitable for monitoring purposes, and under some conditions, may have value for mass trapping (Byers et al. 2017). Research is underway to identify natural enemies that may be useful as biological control agents against *E. formicatus*, but to date, no such agent is available for release (Mendel et al. 2017). Even if a potentially suitable agent can be found, it would take at least a decade before releases could be realized and long before any significant reduction in propagule pressure could be expected. Within agriculture, an economic management option with some promise is to follow careful orchard sanitation practices, such as the removal of infested branches from trees or entire infested trees (Mendel et al. 2017). In essence, this procedure reduces propagule pressure and reduces the chances of heavy infestations. A similar protocol could also likely yield good results in forestry plantations. For this reason, we recommend that heavily infested reproductive host trees in urban settings be removed. These trees are seen as ‘amplifier’ trees that substantially enhance propagule pressure and thus increase future impacts

on neighboring trees. This approach, however, adds additional costs for the appropriate disposal of infested material (e.g., chipping followed by composting, incineration, or solarization, Jones and Paine 2015, Chen et al. 2020). Currently, the most promising method of control of light infestations on individual trees is to apply insecticides and fungicides through direct injection into the tree. This application method maximizes impact while reducing the chances of environmental contamination (Eatough et al. 2017, Mayorquin et al. 2018, Grosman et al. 2019). These methods are currently being investigated in South Africa but are expensive and time-consuming, and the risk of negative impacts on the environment and humans still remains. A report by the California Forest Pest Council (2020) highlights that chemical treatment of infested trees in Orange County currently requires repeated applications (up to three times per year) using a combination of insecticides and fungicides, and various application methods. Such chemical treatment is only an option for high-value trees in urban, agricultural, or forestry settings. It has also been shown that treatment is only beneficial during the early stages of attack; once trees are heavily infested, chemical treatments are ineffective (Mayorquin et al. 2018).

Developing a Strategy

A strategy to protect the standing stock of especially urban trees, but also agricultural and commercial forestry species, against invasion is in the best interest of national-level policymakers, municipalities, and citizens. As a consequence of urban tree invasion by the emerald ash borer, for example, municipal forestry budgets in the United States increased noticeably, but with less spending on urban tree care (pruning, watering, fertilization) and safety training (Hauer and Peterson 2017). With municipalities in South Africa struggling with limited resources and weak accountability, it is unrealistic to expect that budgets for urban tree management could be increased substantially without impacting on the provision of other municipal services (Auditor-General South Africa 2019). The implication is that much of the unmitigated costs of *E. fornicatus* invasion will be borne directly by citizens through expenditure on tree removal and by a loss of urban tree ecosystem services while dead and impacted trees are replaced by trees that would not be suitable hosts for *E. fornicatus*. Several studies have indicated that the additional costs of managing the standing stock of susceptible urban trees to prevent these from being infested weigh up favorably against the additional benefits provided through ecosystem services (McPherson 2003, McPherson et al. 2017). Similar empirical studies are required for South African urban tree species in various municipalities to provide a rationale for the proactive management of susceptible trees.

A coordinated strategy to deal with *E. fornicatus* in South Africa will require a revision of legislation and the creation of policies relating to biological invasions. Currently, there is no coordinated management of invasive species in urban ecosystems (Potgieter et al. 2020), a critical oversight. More generally, the lack of overarching national government policy on biological invasions in South Africa has been highlighted as an important gap (Lukey and Hall 2020), resulting in insufficient intergovernmental coordination among environmental authorities and other organs of state responsible for biological invasions (Zengeya and Wilson 2021). The governance of invasive species in general, and *E. fornicatus* in particular, would require active collaboration between various spheres of government and enhanced involvement of private actors. For example, given the multiple sectors affected by *E. fornicatus*, cross-sectoral coordination will be essential on aspects such as movement, removal, and disposal of infested wood and the destruction of heavily infested

reproductive host trees (Paap et al. 2020). A national strategic framework has recently been developed to achieve this and has been endorsed by national government departments (Christie 2020). It aims to facilitate *E. fornicatus* management in urban and peri-urban environments by supporting municipalities in the removal and safe disposal of heavily infested reproductive hosts. It provides a plan for stakeholder engagement and a public awareness campaign, and highlights the need for ongoing monitoring and research to underpin management strategies. A barrier is that *E. fornicatus* is not yet listed under South Africa's invasive and alien species regulations, but emergency listing of *E. fornicatus* has been proposed (Zengeya and Wilson 2021). *E. fornicatus* has, however, been declared a quarantine pest of agricultural host plants under the Agricultural Pests Act 1983 (Act No. 36 of 1983) (Zengeya and Wilson 2021), and control measures were recently gazetted. The amendment of California's Invasive Species Bill to include invasive shot hole borers (California Legislature 2018) has supported the management of these species in California's urban and natural forests (Coleman et al. 2019). It is hoped that similar actions in South Africa will support the development and implementation of control measures against this damaging invasive species.

Limitations

There are several limitations to the analysis and modeling presented in this paper. Although we believe that our collaborative interdisciplinary approach has produced a set of robust ranges in the modeling parameters, large uncertainties remained, especially pertaining to urban tree invasion and management. Work is needed to gather empirical data on the private costs of not only the removal but also the treatment and replacement of impacted urban trees, as well as local values for ecosystem services. The benefit-transfer method we have used to estimate the ecosystem values of urban trees is accepted in environmental economic literature but is seen as the next-best solution when no local valuation studies are available. Another limitation is the selection of tree species for our analysis. Although we believe that a focus on avocados, wattle, primary forest, and urban forests accounts for most impacts at the national level in South Africa, there may well be other substantial impacts. Pecan (genus *Carya*), macadamia (genus *Macadamia*), castor oil (genus *Ricinus* L. [Malpighiales: Euphorbiaceae]), and litchi (genus *Litchi* Sonn. [Sapindales: Sapindaceae]) were not included as there is no evidence yet to suggest there will be major impacts. Blackwood (*Acacia melanoxylon* R.Br. [Fabales: Fabaceae]) has a potential 5% mortality rate due to *E. fornicatus* but no economic data are currently available so this species was not included in our model. For wattle and avocado, we counted only the private costs. The external costs due to *E. fornicatus* were assumed to be zero, but this is not correct as loss of trees on private land does have negative societal impacts. However, we do not think the loss of these commercial and agricultural trees would have a large societal loss beyond the loss in production value. Finally, it must be noted that the analysis was not an economy-wide damage assessment. Such an assessment would need to include indirect and induced effects throughout the broader economy.

The system dynamics model used provides flexibility when dealing with both qualitative and quantitative interdisciplinary inputs, and provides a strong modeling architecture for simulating alternative outcomes when key parameters are changed. The aim is to build a model following an interactive process until sufficient confidence is generated in the model outputs that these may be deemed usable. A limitation of this modeling approach is that

the mutualism model selected assumes an exponential increase in *E. fornicatus* and *Fusarium* populations. Over our 10-year modeling horizon, we feel that this probably produces reasonable estimates of population growth. However, if the time frame of the model was extended, the assumption of exponential growth would be unrealistic. *E. fornicatus* and *Fusarium* are likely to reach carrying capacity at some stage if left unchecked. However, we have no reliable information to assume when and how this will happen, hence our choice of a time frame of a maximum of 10 yr. Rigorous testing of the model was precluded by a lack of data, but validation is reported in [Supp. Appendix 1 \(online only\)](#).

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Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

References Cited

- Adams, D. C., A. Susaeta, J. R. Soto, F. Rossi, P. C. de Grammont, W. A. Messina, F. H. Koch, D. Gomez, and J. Hulcr. 2020. A bioeconomic model for estimating potential economic damages from a hypothetical Asian beetle introduced via future trade with Cuba. *J. Bioeconomics*. 22: 33–58.
- Auditor-General South Africa. 2019. Consolidated general report on the local government audit outcomes, pp. 1–208. *MFMA 2018-19*. Auditor-General of South Africa, Pretoria, South Africa.
- Aukema, J. E., B. Leung, K. Kovacs, C. Chivers, K. O. Britton, J. Englin, S. J. Frankel, R. G. Haight, T. P. Holmes, and A. M. Liebhold. *et al.* 2011. Economic impacts of non-native forest insects in the continental United States. *PLoS One* 6: 24587.
- Brenner, J., J. A. Jiménez, R. Sardá, and A. Garola. 2010. An assessment of the non-market value of the ecosystem services provided by the Catalan coastal zone, Spain. *Ocean Coast Manag* 53: 27–38.
- Byers, J. A., Y. Maoz, and A. Levi-Zada. 2017. Attraction of the *Euwallacea* sp. near *fornicatus* (Coleoptera: Curculionidae) to quercivorol and to infestations in avocado. *J. Econ. Entomol.* 110: 1512–1517.
- California Forest Pest Council. 2015. California Forest Pest Conditions. (<http://caforestpestcouncil.org/wp-content/uploads/2010/03/fseprd503531.pdf>) (accessed 16 March 2022).
- California Forest Pest Council. 2020. California Forest Pest Conditions. (https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd896758.pdf) (accessed 16 March 2022).
- California Legislature. 2018. AB-2470 Invasive Species Council of California. (https://leginfo.ca.gov/faces/billTextClient.xhtml?bill_id=201720180AB2470) (accessed 16 March 2022).
- Caffrey, J. M., J. R. Baars, J. H. Barbour, P. Boets, P. Boon, K. Davenport, J. T. Dick, J. Early, L. Edsman, and C. Gallagher. *et al.* 2014. Tackling invasive alien species in Europe: the top 20 issues. *Manag. Biol. Invasions* 5: 1–20.
- Chan, J. M., P. Day, J. Feely, R. Thompson, K. M. Little, and C. H. Norris. 2015. *Acacia mearnsii* industry overview: current status, key research and development issues. *South. For.* 77: 19–30.
- Chen, Y., T. W. Coleman, A. L. Poloni, L. Nelson, and S. J. Seybold. 2020. Reproduction and control of the invasive polyphagous shot hole borer, *Euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae), in three species of hardwoods: effective sanitation through felling and chipping. *Environ. Entomol.* 49: 1155–1163.
- Christie, S. 2020. *Strategic Framework for the integrated management of the invasive shot hole borer—Fusarium complex in urban and peri-urban environments. Version 1.1*. Department of Agriculture Land Reform and Rural Development (DALRRD) and Department of Forestry, Fisheries and Environment (DFFE), Pretoria, South Africa.
- CIESIN (Center for International Earth Science Information Network). 2013. Urban-Rural Population and Land Area Estimates Version 2. Palisades, New York. NASA Socioeconomic Data and Applications Center (SEDAC) <https://data.worldbank.org/indicator/AG.LND.EL5M.UR.ZS?locations=ZA>.
- Coleman, T. W., A. L. Poloni, Y. Chen, P. Q. Thu, Q. Li, J. Sun, R. J. Rabaglia, G. Man, and S. J. Seybold. 2019. Hardwood injury and mortality associated with two shot hole borers, *Euwallacea* spp., in the invaded region of southern California, USA, and the native region of Southeast Asia. *Ann. For. Sci.* 76: 1–18.
- Department of Agriculture, Forestry and Fisheries (DAFF). 2020. *Abstract of Agricultural Statistics 2019 [Excel spreadsheet]*. Government Printer, Pretoria, South Africa.
- De Groot, R. S., J. Blignaut, S. van der Ploeg, J. Aronson, T. Elmqvist, and J. Farley. 2013. Benefits of investing in ecosystem restoration. *Conserv. Biol.* 27: 1286–1293.
- De Groot, R., L. Brander, S. van der Ploeg, R. de Groot, L. Brander, S. van der Ploeg, R. Costanza, F. Bernard, L. Braat, M. Christie. *et al.* 2012. Global estimates of the value of ecosystems and their services in monetary units. *Ecosyst. Serv.* 1: 50–61.
- Eatough, J. M., J. Kabashima, A. Eskalen, M. Dimson, J. S. Mayorquin, J. D. Carrillo, C. C. Hanlon, and T. D. Paine. 2017. Evaluations of insecticides and fungicides for reducing attack rates of a new invasive ambrosia beetle (*Euwallacea* sp., Coleoptera: Curculionidae: Scolytinae) in infested landscape trees in California. *J. Econ. Entomol.* 10: 1611–1618.
- Eskalen, A., A. Gonzalez, D. H. Wang, M. Twizeyimana, J. S. Mayorquin, and S. C. Lynch. 2012. First report of a fusarium sp. and its vector tea shot hole borer (*Euwallacea fornicatus*) causing fusarium dieback on avocado in California. *Plant Dis.* 96: 1070.
- Eskalen, A., R. Stouthamer, S. C. Lynch, P. F. Rugman-Jones, M. Twizeyimana, A. Gonzalez, and T. Thibault. 2013. Host range of *Fusarium* dieback and its ambrosia beetle (Coleoptera: Scolytinae) vector in southern California. *Plant Dis.* 97: 938–951.
- Euler, L. 1741. Solutio problematis ad geometriam situs pertinentis. *Comm. Acad. Scient. Imp. Petrop.* 8: 128–140.
- Eurostat and, OECD. 2007. *Eurostat-OECD Methodological Manual on Purchasing Power Parities, Annex VII, Glossary of terms and abbreviations*. OECD, Paris. www.oecd.org/sdd/prices-ppp/PPP%20manual%20revised%202012.pdf
- Evans, E. A., J. Crane, A. Hodges, and J. L. Osborne. 2010. Potential economic impact of laurel wilt disease on the Florida avocado industry. *HortTechnology* 20: 234–238.
- Fortunato, S. 2010. Community detection in graphs. *Phys. Rep.* 486: 75–174.
- Freeman, S., M. Sharon, M. Maymon, Z. Mendel, A. Protasov, T. Aoki, A. Eskalen, and K. O'Donnell. 2013. *Fusarium euwallaceae* sp. nov.—a symbiotic fungus of *Euwallacea* sp., an invasive ambrosia beetle in Israel and California. *Mycologia* 105: 1595–1606.
- Gomez, D. F., W. Lin, L. Gao, and Y. Li. 2019. New host plant records for the *Euwallacea fornicatus* (Eichhoff) species complex (Coleoptera: Curculionidae: Scolytinae) across its natural and introduced distribution. *J. Asia-Pac. Entomol.* 22: 338–340.
- Grosman, D. M., A. Eskalen, and C. Brownie. 2019. Evaluation of emamectin benzoate and propiconazole for management of a new invasive shot hole borer (*Euwallacea* nr. *fornicatus*, Coleoptera: Curculionidae) and symbiotic fungi in California sycamores. *J. Econ. Entomol.* 112: 1267–1273.
- Grousset, F., J. C. Grégoire, H. Jactel, A. Battisti, A. B. Beloglavec, B. Hrašovec, J. Hulcr, D. Inward, A. Orlinski, and F. Petter. 2020. The risk of bark and ambrosia beetles associated with imported non-coniferous wood and potential horizontal phytosanitary measures. *Forests* 11: 1–17.

- Guild, J., and C. M. Shackleton. 2018. Informal urban fuelwood markets in South Africa in the context of socio-economic change. *Energy Policy* 117: 136–141. doi:10.1016/j.enpol.2018.03.023.
- Hauer, R. J., and W. D. Peterson. 2017. Effects of emerald ash borer on municipal forestry budgets. *Landsc Urban Plan* 157: 98–105.
- Holmes, T. P., J. E. Aukema, B. Von Holle, A. Liebhold, and E. Sills. 2009. Economic impacts of invasive species in forests: past, present, and future. *Ann. N. Y. Acad. Sci.* 1162: 18–38.
- IMF. 2021. *World Economic Outlook Database (October 2021)*. (<https://www.imf.org/en/Publications/WEO/Issues/2021/10/12/world-economic-outlook-october-2021>) (accessed 22 October 2021).
- Jones, M. E., and T. D. Paine. 2015. Effect of Chipping and solarization on emergence and boring activity of a recently introduced ambrosia beetle (*Euwallacea* sp., Coleoptera: Curculionidae: Scolytinae) in southern California. *J. Econ. Entomol.* 108: 1852–1859.
- Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecol. Econ* 69: 569–578.
- Kovacs, K. F., R. J. Mercader, R. G. Haight, N. W. Siegert, D. G. McCullough, and A. M. Liebhold. 2011. The influence of satellite populations of emerald ash borer on projected economic costs in U.S. communities, 2010–2020. *J. Environ. Manage.* 92: 2170–2181.
- Leathers, J. 2015. California pest rating for *Euwallacea* sp. nr. *formicatus*: polyphagous shot hole borer (*E. formicatus*), Coleoptera: Curculionidae, pest rating: B. (<http://blogs.cdfa.ca.gov/Section3162/?tag=polyphagous-shot-hole-borer>) (accessed 18 December 2020).
- Lynn, K. M. T., M. J. Wingfield, A. Durán, S. Marincowitz, L. S. S. Oliveira, Z. W. de Beer, and I. Barnes. 2020. *Euwallacea perbrevis* (Coleoptera: Curculionidae: Scolytinae), a confirmed pest on *Acacia crassicaarpa* in Riau, Indonesia, and a new fungal symbiont: *Fusarium rekanum* sp. nov. Antonie van Leeuwenhoek, *Int. J. Gen. Mol. Microbiol.* 113: 803–823.
- Lukey P., and J. Hall. 2020. Biological invasion policy and legislation development and implementation in South Africa, pp. 513–548. In: B.W. van Wilgen, J. Measey, D.M. Richardson, J.R. Wilson, and T.A. Zengeya (eds.) *Biological invasions in South Africa*. Springer, Cham, Switzerland.
- Mayorquin, J. S., J. D. Carrillo, M. Twizeyimana, B. B. Peacock, K. Y. Sugino, F. Na, D. H. Wang, J. N. Kabashima, and A. Eskalen. 2018. Chemical management of invasive shot hole borer and *Fusarium* dieback in California sycamore (*Platanus racemosa*) in southern California. *Plant Dis.* 102: 1307–1315.
- McPherson, E. G. 2003. A benefit-cost analysis of ten tree species in Modesto, California, U.S.A. *J. Arboric.* 29: 1–8.
- McPherson, E. G., Q. Xiao, N. S. van Doorn, J. de Goede, J. Bjorkman, A. Hollander, R. M. Boynton, J. F. Quinn, and J. H. Thorne. 2017. The structure, function and value of urban forests in California communities. *Urban For Urban Green* 28: 43–53.
- Mendel, Z., A. Protasov, Y. Maoz, M. Maymon, G. Miller, M. Elazar, and S. Freeman. 2017. The role of *Euwallacea* nr. *formicatus* (Coleoptera: Scolytinae) in the wilt syndrome of avocado trees in Israel. *Phytoparasitica* 45: 341–359.
- Mendel, Z., A. Protasov, M. Sharon, A. Zveibil S. B. Yehuda, K. O'Donnell, R. Rabaglia, M. Wysoki, and S. Freeman. 2012. An Asian ambrosia beetle *Euwallacea formicatus* and its novel symbiotic fungus *Fusarium* sp. pose a serious threat to the Israeli avocado industry. *Phytoparasitica*. 40: 235–238.
- Mongabay, 2011. South Africa forest information and data. (https://rainforests.mongabay.com/deforestation/2000/South_Africa.htm) (accessed 11 June 2020)
- Mosquera, M., E. Evans, and R. Ploetz. 2015. Assessing the profitability of avocado production in south Florida in the presence of laurel wilt. *Theoret. Econ. Lett.* 5: 343–356.
- NCT Forestry Co-Operative Ltd, 2014. News and Views No. 84 April 2014. (<http://www.nctforest.com/upload/Publications/News%20n%20Views%20April%202014%20electronic.pdf>) (accessed 23 November 2020).
- Oberholzer, F., and R. Godsmark. 2020. Forestry South Africa roundwood sales analysis for 2019 financial year. *Presentation by Forestry South Africa*, January, pp 1–31.
- O'Donnell, K., R. Libeskind-Hadas, J. Hulcr, C. Bateman, M. T. Kasson, R. C. Ploetz, J. L. Konkol, J. N. Ploetz, D. Carrillo, and A. Campbell. *et al.* 2016. Invasive Asian *Fusarium*—*Euwallacea* ambrosia beetle mutualists pose a serious threat to forests, urban landscapes and the avocado industry. *Phytoparasitica* 44: 435–442.
- O'Donnell, K., S. Sink, R. Libeskind-Hadas, J. Hulcr, M. T. Kasson, R. C. Ploetz, J. L. Konkol, J. N. Ploetz, D. Carrillo, and A. Campbell. *et al.* 2015. Discordant phylogenies suggest repeated host shifts in the *Fusarium*-*Euwallacea* ambrosia beetle mutualism. *Fungal Genet. Biol.* 82: 277–290.
- Orbay, L., J. A. McLean, B. J. Sauder, and P. L. Cottell. 1994. Economic losses resulting from ambrosia beetle infestation of sawlogs in coastal British Columbia, Canada. *Can. J. For. Res.* 24: 1266–1276.
- Owens, D., M. Seo, W. S. Montgomery, M. J. Rivera, L. L. Stelinski, and P. E. Kendra. 2019. Dispersal behaviour of *Euwallacea* nr. *formicatus* (Coleoptera: Curculionidae: Scolytinae) in avocado groves and estimation of lure sampling range. *Agric. For. Entomol.* 21: 199–208.
- Paap, T., Z. W. de Beer, D. Migliorini, W. J. Nel, and M. J. Wingfield. 2018. The polyphagous shot hole borer (*E. formicatus*) and its fungal symbiont *Fusarium euwallaceae*: a new invasion in South Africa. *Australas. Plant Pathol.* 47: 231–237.
- Paap, T., M. J. Wingfield, Z. W. de Beer, and F. Roets. 2020. Lessons from a major pest invasion: The polyphagous shot hole borer in South Africa. *S. Afr. J. Sci.* 116: Art. #8757.
- Peper, P., E. G. McPherson, J. R. Simpson, S. L. Gardner, K. E. Vargas, and Q. Xiao. 2007. Municipal Forest Resource Analysis. Technical report, Department of Parks and Recreation, New York City, New York.
- Potgieter, L., E. Douwes, M. Gaertner, *et al.* 2020. Biological invasions in South Africa's urban ecosystems: Patterns, processes, impacts and management, pp. 275–309. In: B.W. van Wilgen, J. Measey, D.M. Richardson, J.R. Wilson, and T.A. Zengeya (eds.) *Biological invasions in South Africa*. Springer, Cham.
- Rabaglia, R. J., S. A. Dole, and A. I. Cognato. 2006. Review of American *Xyleborina* (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. *Ann. Entomol. Soc. Am.* 99: 1034–1056.
- Rugman-Jones, P. F., M. Au, V. Ebrahimi, A. Eskalen, C. P. Gillett, D. Honsberger, D. Husein, M. G. Wright, F. Yousuf, and R. Stouthamer. 2020. One becomes two: second species of the *Euwallacea formicatus* (Coleoptera: Curculionidae: Scolytinae) species complex is established on two Hawaiian Islands. *PeerJ* 8: e9987.
- Saplaco, R., and H. Francisco. 1993. ValuAsia: Benefits Transfer for Southeast Asia. *EEPSEA Special and Technical Paper, No sp199301t2, Economy and Environment Program for Southeast Asia (EEPSEA)*. (<https://EconPapers.repec.org/RePEc:eep:tpaper:sp199301t2>) (accessed 12/02/2021).
- Schäffler, A., N. Christopher, K. Bobbins, E. Otto, M. Nhlozi, M. de Wit, H. van Zyl, D. Crookes, G. Gotz, and G. Trangoš, *et al.* 2013. *State of green infrastructure in the Gauteng City-Region, GCRO Report*. Gauteng City-Region Observatory, Johannesburg.
- Soares, A. L., F. C. Rego, E. G. McPherson, J. R. Simpson, P. J. Peper, and Q. Xiao. 2011. Benefits and costs of street trees in Lisbon, Portugal. *Urban For Urban Green* 10: 69–78.
- Sterman, J. 2000. *Business dynamics: systems thinking and modelling for a complex world*. Irwin/McGraw-Hill, Boston.
- Stouthamer, R., P. Rugman-Jones, P. Q. Thu, A. Eskalen, T. Thibault, J. Hulcr, L. -J. Wang, B. H. Jordal, C. -Y. Chen, and M. Cooperband. *et al.* 2017. Tracing the origin of a cryptic invader: phylogeography of the *Euwallacea formicatus* (Coleoptera: Curculionidae: Scolytinae) species complex. *Agric. For. Entomol.* 19: 366–375.
- Susaeta, A., J. R. Soto, D. C. Adams, and J. Hulcr. 2016. Pre-invasion economic assessment of invasive species prevention: a putative ambrosia beetle in Southeastern loblolly pine forests. *J. Environ. Manage.* 183: 875–881.
- Thu, P. Q., D. N. Quang, N. M. Chi, T. X. Hung, L. V. Binh, and B. Dell. 2021. New and emerging insect pest and disease threats to forest plantations in Vietnam. *Forests* 12: 1301.

- Treepedia. 2020. Exploring the green canopy in cities around the world. <http://senseable.mit.edu/treepedia/cities/cape%20town> (accessed on 23 November 2020).
- Touza, J., K. Dehnen-Schmutz, and G. Jones. 2007. Economic analysis of invasive species policies, pp. 353–366. In W. Nentwig (ed.), *Biological Invasions*. Springer, Berlin.
- Turpie, J. K., K. J. Forsythe, A. Knowles, J. Blignaut, and G. Letley. 2017. Mapping and valuation of South Africa's ecosystem services: a local perspective. *Ecosyst. Serv.* 27: 179–192.
- van Rooyen, E., T. Paap, Z. W. de Beer, G. Townsend, S. Fell, W.J. Nel, S. Morgan, M. Hill, A. Gonzales, and F. Roets. 2021. The polyphagous shot hole borer (*E. formicatus*) beetle: current status of a perfect invader in South Africa. *S. Afr. J. Sci.* 117(11/12), Art. #9736.
- van Zyl, J. L., and S. G. Ferreira. 1995. An Overview of the avocado industry in South Africa. *South African Avocado Growers' Association Yearbook* 18: 23–30.
- Ventana Systems, Inc. 2015. Vensim User Guide & Software, Harvard, MA. (<http://www.vensim.com>) (accessed 07 July 2020).
- Wilson J.R., D.F. Panetta and C. Lindgren. 2017. *Detecting and responding to alien plant incursions*. Cambridge University Press, Cambridge, United Kingdom.
- World Bank. 2020. World Development Indicators. (<https://data.worldbank.org/country/ZA>) (accessed 13 November 2020).
- Zengeya, T. A., and J. R. Wilson. 2021. *The status of biological invasions and their management in South Africa in 2019*. South African National Biodiversity Institute, Kirstenbosch and DSI-NRF Centre of Excellence for Invasion Biology, Stellenbosch, South Africa.