Invasion of the Polyphagous Shot Hole Borer Beetle in South Africa A Preliminary Assessment of the Economic Impacts

Martin P de Wit (✉ mdewit@sun.ac.za)

Stellenbosch University School of Public Leadership <https://orcid.org/0000-0003-3054-2479>

Douglas J Crookes

Stellenbosch University, School of Public Leadership

James N Blignaut

Stellenbosch University, School of Public Leadership

Z Wilhelm de Beer

University of Pretoria Forestry and Agricultural Biotechnology Institute

Trudy Paap

University of Pretoria Forestry and Agricultural Biotechnology Institute

Francois Roets

Stellenbosch University Department of Conservation Ecology and Entomology

Carmen van der Merwe

Stellenbosch University Department of Economics

Dave M Richardson

Stellenbosch University DST-NRF Centre of Excellence for Invasion Biology

Research Article

Keywords: Ambrosia beetles, economic assessment, ex ante decision support, municipal governance, system dynamics modelling

Posted Date: February 23rd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-220132/v1>

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Abstract

Few economic assessments have been developed to inform national priorities on the management of high-impact, early-stage invasive alien species (IAS). Economic assessments are biased towards *ex post* assessments of the costs and benefits of control options and are in need of refinement to deal with potentially vigorous invaders with considerable uncertainty on spread and impact. The Polyphagous Shot Hole Borer (PSHB) beetle represents a potentially high-impact invasion in progress in South Africa. We approached the problem of PSHB invasion in South Africa through (i) interdisciplinary collaboration to reduce uncertainty in economic and biological parameters by defining robust ranges for model parameters and (ii) a simulation model to take account of dynamic mutualistic relations between the beetle and its symbiont fungus. We modelled the potential social cost of a PSHB invasion on natural forests, urban trees, commercial forestry and the avocado industry. Our results indicate that the unmitigated baseline present social cost of \$27.12bn in the case of a PSHB invasion in South Africa is in the order of 1% of the country's GDP, or expressed differently at around \$50 per year per South African citizen (10-year modelling horizon using a discount rate of 6%). Most of the social costs in our model are for the removal of urban trees that die as a result of the PSHB, a result that corroborates well with findings in other regions where PSHB has invaded. We conclude that an *ex ante* economic assessment system dynamics model can effectively inform national strategies on IAS management. The disproportionately high impacts of a PSHB invasion on municipalities and private actors demands a revision of legislation and creation of policies pertaining to the management of biological invasions in South Africa.

Introduction

Invasive alien species (IAS) have major impacts on agriculture, biodiversity and ecosystem services globally. The rates at which new invasions are emerging show no sign of slowing and the magnitude of impacts is increasing (Pyšek et al. 2020). Despite major advances in our ability to predict aspects of the dynamics of biological invasions, invasions of complex social-ecological systems make predictions difficult complex (Hui and Richardson 2017). Major surprises still arise and present considerable challenges for managers and planners, also in South Africa. This is despite the fact that South Africa has a long history of innovative approaches for dealing with biological invasions. Like other countries, it also needs to remain vigilant and deal with the constant threats posed by new invasions (Van Wilgen et al. 2020a).

IAS are ecologically undesirable, and in many cases cause substantial losses to the economy and society at large (Pejchar and Mooney 2009; Pimentel 2011; Marbuah et al. 2014). Economic assessments on invasive alien plants at the species level, also in South Africa, have indicated that benefits of control outweigh the costs in most cases, especially when broader societal costs are included (De Wit et al. 2001; McConnachie et al. 2003; Van Wilgen et al. 2004, 2020b; Wise et al. 2012; Crookes et al. 2020). The benefits of controlling plant invasions were pivotal in motivating for the launch of the largest

environmental management programme in Africa – the Working for Water programme (Van Wilgen et al. 2001).

A recent addition to the long list of invasive species that cause major impacts in South Africa is the Polyphagous Shot Hole Borer beetle (PSHB), *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) and its fungal symbiont, *Fusarium euwallaceae* (Hypocreales: Nectriaceae). This beetle, native to South-East Asia (Stouthamer et al. 2017), has invaded agricultural, urban and native systems 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 Durban in 2012 [Barcode of Life project (BOLD: ACC9773, ETKC270–13)] (Stouthamer et al. 2017). The significance of that record was, however, only established in 2017 when specimens were found infesting London plane trees (*Platanus x acerifolia*) in a botanical garden in Pietermaritzburg (Paap et al. 2018). Since then the beetle 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.

The international literature shows that PSHB is a particularly vigorous invader. It affects a wide range of trees across various landscapes, with urban forests being especially vulnerable (Eskalen et al. 2013). Economic sectors, including the avocado and plantation forestry industries (Mendel et al. 2012; Hulcr et al. 2017), are also impacted. Given that the invasion in South Africa is at an early stage, very little is known about both its current and possible unmitigated spread and impact. As has been the case in other parts of the world (Gaertner et al. 2017), little attention has been paid to assessing the impacts of biological invasions in urban ecosystems of South Africa (Potgieter et al. 2020). One source estimates that if all of Johannesburg's 10 million urban trees are affected, it may have an impact of over R50bn if these trees need to be removed, chopped, chipped and replanted with more resistant species (DAFF 2020a). While we believe that these suggested impacts are significantly overstated we support a call for attention to the potential threat of a PSHB invasion on urban trees in South Africa. These estimates are, however, based on a small geographic area and with limited information on the host status of most tree species in the country. The potential extent and scale of impacts, including economic consequences, are unknown. *Ex post* economic assessments based on actual impacts are thus not feasible. The real-world management and policy questions that decision makers are facing regarding IAS highlight the limitations of the economic assessment tools that were developed initially (Van Wilgen et al. 2001; Turpie 2004; Born et al. 2005; Dana et al. 2013). Refinements in the following three main directions are needed to address the problem: (i) providing simple and standardized assessment tools; (ii) being able to deal with sparse information in rapidly changing situations; and (iii) providing *ex ante* (based on forecasts) rather than *ex post* (based on actual results) decision support.

Economics is crucial for understanding biological invasions, not only in recognising how economic activities drive the introduction and spread of IAS, and how public and private choices affect invasions, but also for developing tools to evaluate IAS policies and regulation to achieve social objectives in an economically efficient manner (Epanchin-Niell 2017). Economic assessment is a well-documented tool for calculating potential costs and anticipated benefits to projects, programmes or policies, and has

many applications in invasion science and biosecurity. The conceptually simple cost-benefit analysis framework can be used effectively to prioritize multiple invasive species under limited budgets (Courtois et al. 2018). A limitation of cost-benefit analysis when used as a static tool is that it cannot deal adequately with ecological and economic dynamics (Turpie 2004), but it has been shown empirically that temporal patterns of damages do have a crucial impact on the magnitude of damages calculated in economic assessments (Epanchin-Niell and Liebhold 2015). To counter the bias in favour of short-term damage assessments, simulation modelling and scenario-based approaches have been used in IAS management, but these have focussed mainly on the control of IAS (Higgins et al. 1997a,b; De Wit et al. 2001). Using simulation modelling in support of economic assessment provides the means to present the costs of IAS and the benefits of control under various scenarios and over different time horizons. In this context, standard cost-benefit analysis can still be used as a theoretical framework, but we can now include simulations of ecological and economic dynamics revealing probable system trajectories over time. The value of this approach has been demonstrated in several natural resource and environmental management applications including some involving biological invasions (Mudavanhu et al. 2017a,b; Vundla et al. 2017; Bester et al. 2019; Nkambule et al. 2017), but also ecological restoration (Crookes et al. 2013), aquaculture management (Nobre et al. 2009) and irrigation farming (De Wit and Crookes 2013). A similar approach that integrates cost-benefit analysis and simulation modelling is followed in this paper.

A further area of refinement for economic assessment tools in invasion science is the ability to deal with sparse information in potentially rapidly changing situations. Most economic research has focussed on estimating the impacts of IAS and developing optimal prevention and control strategies using cost-benefit and bioeconomic modelling approaches (Epanchin-Niell 2017). To deal with uncertainty the usual economic approach is to optimize investments by calculating expected utility or to follow Bayesian approaches (Aukema et al. 2011; Epanchin-Niell 2017). In reality, uncertainty about invasions is often too severe to make such approaches feasible, and simply using a sensitivity analysis on model assumptions may be more appropriate (Epanchin-Niell 2017). Lack of data needed for economic analysis and lack of collaboration between invasive species scientists and economists has been flagged as a serious limitation in IAS management; this was ranked as one of the Top 20 IAS issues 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); we follow this approach in this paper.

There is a strong need to develop economic assessment tools to support decision making *ex ante* to deal with invasions in progress. Studies on the economic evaluation of biological invasions do not provide equal levels of support on which to base decisions pertinent to all stages of the introduction-naturalization-invasion continuum (including prevention, early detection, rapid response and eradication, control or mitigation and adaptation), but are biased towards control. Such *ex post* economic assessment has traditionally been the focus of most research, but this approach is less suitable for the development of national strategies on IAS (Born et al. 2005), specifically for potentially high-impact invaders that are at an early stage in the invasion process, such as PSHB. *Ex ante* assessments, or those

assessments focussed on prevention, are less common, but most of those that have been done have used integrated ecological-economic models (e.g. Higgins et al. 1997a,b) or bioeconomic models that account for feedback between the biological and economic systems (e.g. Finnoff et al. 2005), and play an important role in early planning and the prioritisation of resources to deal with new invaders. *Ex ante* approaches include a preliminary estimation of damages while accounting for dynamics and uncertainty and provides good value to prioritising investments in rapid response and eradication of early outbreaks. It has been argued, for example, that investing in a better understanding of the potential damage of IAS yields more benefits to society than the costs of rapid response and early eradication of IAS done to avoid potentially larger damage and control costs in the future (Marbuah et al. 2014).

This study aims to develop a preliminary economic assessment for early-phase IAS characterised by potentially high economic impacts and damage costs, where little information is available on biological dynamics and where there is considerable uncertainty on spread and impacts. The approach is novel in combining standard economic assessment approaches with expert opinion in invasion science in a simulation modelling approach. The benefit of such an approach is that it provides more concrete assistance in the development of potential strategies, policies and legislation on IAS.

Study species

Ambrosia beetles (Coleoptera: Curculionidae: Scolytinae; tribe Xyleborini) are emerging as globally important invasive species (Ploetz et al. 2013; Brockerhoff and Liebhold 2017; Lantschner et al. 2020). Reasons for their success as invaders include their cryptic ecologies and biologies, their haplodiploid mating system, and the broad plant host range in which fungal symbionts can establish (Gomez et al. 2018). Their global spread has been facilitated by their frequent presence in wood packaging material (Brockerhoff et al. 2006). Once established, the spread of alien ambrosia beetles is facilitated by anthropogenically-mediated dispersal, especially by movement of infested wood (Gomez et al. 2018). Most species colonize dead and dying plants and only a small proportion of ambrosia beetles are capable of infesting healthy hosts; among those that have this capacity are the four lineages in the *Euwallacea fornicatus sensu lato* complex (Hulcr and Stelinski 2017).

Euwallacea fornicatus (Fig. 2a) is a minute ambrosia beetle (ca. 2mm in length) that has a symbiotic relationship with three fungal species. It constructs galleries in susceptible host trees and inoculates these with its fungal symbionts (including the pathogen *Fusarium euwallaceae*) which serve as the primary food source for adults and larvae (Eskalen et al. 2013; Freeman et al. 2013; O'Donnell et al. 2015). Successful colonization of hosts can lead to Fusarium dieback, a disease that causes branch dieback and, in some species, tree death. 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 (Fig 2b – d). As a result, the host range for the beetle and its fungus is amongst the widest of all tree-killing invasive beetles in the world. In South Africa, the fungus has been found to establish in more than 100 different plant species and the beetle can colonize (and likely kill) at least 30 of these (ZW De Beer, T Paap, F Roets unpubl data). The hosts in which the beetle can reproduce include major agricultural crops (e.g. avocado; *Persea*

americana), important plantation forestry trees (e.g. black wattle; *Acacia mearnsii*), a large number of ecologically important native trees (e.g. *Virgilia oroboides* and *Erythrina* spp.), and important urban forest species such as London plane (*Platanus x acerifolia*) and English oak (*Quercus robur*) (ZW De Beer, T Paap, F Roets unpubl data; Fig 2 b – h).

Following colonization by PSHB and *F. euwallaceae*, the combination of fungal growth in tree tissue and mechanical damage resulting from beetle tunnelling can weaken trees. Stems and branches weakened by beetle gallery formation may break or fall, with the potential for major impacts to infrastructure and injury to humans in urban and peri-urban environments. Falling trees may cause traffic accidents and damage vehicles and infrastructure such as buildings, fences and power lines (Fig. 2i). It is predicted that a substantial financial burden will be borne by residents and municipalities in areas where large numbers of heavily infested (dead and dying) trees will have to be removed and disposed of.

Even though the invasion by PSHB in South Africa is recent, it has already infested thousands of trees in urban and native environments. Urban trees are particularly vulnerable to pest invasions; a consequence of high propagule pressure, and the potential for stressful conditions to predispose trees to pest attack (Paap et al. 2017). In urban areas in Johannesburg, George and Somerset West, thousands of dead and dying street trees are actively removed to prevent damage to people and property. This comes at a social cost which includes the cost of tree removal and replacement, but also the loss of the provision of ecosystem services in urban areas (Bolund and Hunhammar 1999; Livesley et al. 2016); for example, mortality due to the emerald ash borer has been associated with relative increases in crime (Kondo et al. 2017).

Thousands of native trees in forests in Durban, Knysna and George are infested by PSHB; many of these are either dead or dying. Losing key native species can lead to major biodiversity loss and to the collapse of stability of many important ecological processes such as forest succession, fire regimes and rates of gap formation. These impacts will be especially damaging considering the limited extent and already severely fragmented nature of forest ecosystems in South Africa (Mucina and Rutherford 2006). Damage to native trees by PSHB has not been assessed at a large scale in any of its invaded ranges globally, but a closely related species, *E. kurisho*, has likely permanently altered the ecological landscape of a river valley in California by devastating the dominant tree species (Boland 2016).

In terms of agriculture, PSHB infestations have been reported in orchards of Pecan nut (*Carya illinoensis*) (Fig 2b) and Macadamia nut (the most widely planted cultivar in South Africa is a hybrid between *Macadamia integrifolia* and *M. tetraphylla* called “Beaumont”), but do not pose any immediate risk to their production (Twiddy et al. 2020). Most concerning is the potential impact this invasion may have on the avocado industry. In Israel, PSHB infestations have led to 100% yield loss in avocado in some instances (Eskalen 2012). Even though no PSHB infestations have been found in commercial avocado orchards in South Africa to date, the potential impact on this industry in the country could be substantial. *Fusarium euwallaceae* has also been isolated from other crop species such as citrus, olive, grape vine, apple, guava and stone fruit, but potential impacts have not yet been assessed.

With regards to plantation forestry species in South Africa, to date PSHB infestations have only been observed on a small number of roadside trees of black wattle (*Acacia mearnsii*), and no trees in commercial plantations are known to have been impacted (Fig 2d). Based on observations on *Acacia* spp. from commercial forestry in SE Asia (Hulcr et al. 2017), however, the threat posed to this species which is an important component of the South African commercial forestry industry is cause for concern. Of note is that *A. mearnsii* is considered one of the most problematic and widespread invasive plant species in South Africa (Richardson et al. 2020). A permitting system exists for its commercial growth, and outside of commercial forestry settings, it must be controlled or eradicated. Despite the threat posed by PSHB to commercial *A. mearnsii*, it is highly unlikely that PSHB will provide any environmental benefit as a biological control agent of invasive trees. As a reproductive host, invasive *A. mearnsii* may allow large numbers of beetles to build up and spread to adjacent agricultural, plantation or natural forest trees (F Roets, T Paap pers obs).

Methods

Modelling philosophy.

We make use of a purpose-built system dynamics model to estimate the potential economic impact of PSHB in South Africa. System dynamics modelling is an approach applied to modelling complex and dynamic systems characterised by non-linear impacts between the components (Sterman 2000). These models involve the development of various stock-flow interactions whereby the level of the stock is determined by in- and out-flows. The relationship between the stock and the flow variable is either positive (also called a reinforcing loop) or negative (a balancing loop). It is positive when a symmetric relationship between the level of the stock and the direction of the flow exists, such as when an increase in the flow leads to an increase in the stock – i.e. births leading to an increase in the population. Conversely, when an asymmetric relationship exists and an increase in the flow leads to a decline in the stock – i.e. an increase in deaths leading to a reduction in the population – then that relationship is negative. The system dynamics model constructed for this study was developed in Vensim DSS version 6.4b (Ventana Systems Inc 2015).

System dynamics models may be developed using system archetypes. These archetypes are typical structures such as patterns of behaviour of a system (Senge 1990). Models could also be developed as stock-flow diagrams that show the quantitative links between elements in the system using mathematical equations. These equations may be derived from population ecology or other known relationships. Lotka-Volterra equations have been used to model parasitism and mutualistic interactions, although their use in system dynamics models for invasive species is sparse. Mutualistic relationships are those in which two or more organisms involved benefit each other's fitness (Traveset and Richardson 2014). As an example, Bendor and Metcalf (2006) used Lotka-Volterra equations in a system dynamics model for the emerald ash borer (EAB) (*Agrilus planipennis*) and its impacts on host ash trees (*Fraxinus* spp.). Crookes et al. (2020) used both Lotka-Volterra equations and a system dynamics modelling approach to model the economic benefits of eradicating invasive alien plants in South Africa. They did so by considering the

relationship between two invasive pine species (*Pinus patula* and *P. pinaster*) and one invasive wattle species (*Acacia mearnsii*) within a multispecies system subject to control efforts.

Table 1 Social cost of tree loss due to infestation by the Polyphagous Shot Hole Borer beetle in South Africa (2019 Int. \$ m).

		Tree mortality		Value per tree		Total social cost of tree loss	
		Million trees lost		Low	High	Low	High
Urban trees	63.75			289.60	3 326.80	18 462.00	212 084.00
Primary forest	71.03			1.41	4.43	100.00	315.00
Wattle	0.14			63.64	91.17	8.70	12.46
Avocados	0.08			592.50	848.80	44.98	64.44

Notes: Low and high values are based on the range of prices and values given in the data section. Comparative static analysis based on the potential number of trees lost over 10 years. No discounting employed; values are not Net Present Values.

The combination of Lotka-Volterra equations and a system dynamics modelling approach is ideally suited for modelling the potential economic impact of PSHB. This is because there is a symbiotic relationship between PSHB and the pathogenic fungus *Fusarium euwallaceae*. Under the Beetle-Fungus Mutualistic Lotka-Volterra System Dynamics (hereafter BF-MLV-SD) model, the symbionts interact with each other and, as a result, grow exponentially (May 1982). In this mutualism model we expect that an increase in the beetles colonizing trees (i.e. reproductive hosts that will more than likely have high mortality) will also lead to an increase in the numbers of hosts that are infected by the fungus only (non-reproductive hosts that may have some mortality, but not much).

Data

To assess the economic impacts of PSHB in South Africa, we obtained values for four focus areas where the largest impacts of PSHB are expected on the basis of expert opinion by the authors and others, namely: the agricultural sector, commercial forestry, natural forests, and urban environments. Natural forests, urban landscapes, commercial forestry and the avocado industry have been identified before as being under threat from *Euwallacea* ambrosia beetles (O'Donnell et al. 2015; Lynn et al. 2020). To determine the monetary values of the trees affected by PSHB in each sector, we outline data collection methods for each area below.

Agricultural Sector

The quantification of numbers of trees lost and the production value lost due to infestations in the agricultural sector focussed on avocado (*Perseaamericana*) – the primary crop tree species affected by

PSHB. Other agricultural tree species impacted by PSHB as reported in global case studies are listed in Table S.1 in the Supplementary Material. These species are excluded in our analysis due to the uncertainty of the impacts of PSHB on these species in a South African context.

PSHB colonization of avocado in Israel has led to yield loss of up to 100% in some instances (Eskalen 2012). However, this is strongly dependent on the susceptibility of the specific variety that is planted and on the control strategies implemented. *Hass* is considered one of the most susceptible varieties in Israel (Eskalen et al. 2012; Mendel et al. 2017); this variety is also one of the most widely planted varieties in South Africa (Van Zyl and Ferreira 1995). Future impacts on this industry are expected to be severe, as no control method has proved fully effective in curbing production loss (Mendel et al. 2017). We decided to conservatively estimate loss in production at 25%

The gross production value (GPV) is the value of production in physical terms multiplied by the output prices at farm gate (producer price). Production values for avocado trees were taken from the Department of Agriculture, Forestry and Fisheries' Agricultural Statistics (DAFF 2020b: 44). The most recently reported GPV for Avocado tree production in South Africa was Int. \$127.79m for the year 2017/2018 (Fig. S1 in Supplementary Material). The GPV of avocado in South Africa has grown over time, and from this it was possible to determine the change in producer price over time. The producer price at the beginning of the time period (Int. \$21 771/t in 2020) and at the end of the time period (Int. \$31 188/t in 2030) formed the basis of the high and low values used in our modelling, whereas the model also incorporated actual changes in price over time, discounted to the present time period.

Commercial Forestry Sector

Of the tree species used in commercial forestry in South Africa, only *Acacia mearnsii* (black wattle) is currently known to be a reproductive host for PSHB. Infestations on this host currently occur only on roadside trees and on isolated individuals on private properties. In general, when beetles are able to breed in a host tree, host trees are likely to experience decline and later death. However, this process can be slow for some host species such as is the case for London plane trees that only start dying after about 5 years of infestations. As populations on *A. mearnsii* are confined to areas that experienced PSHB invasion only fairly recently (e.g. since 2016 in George) and since no tree mortality has yet been detected, we conservatively estimate future tree mortality for *A. mearnsii* at 5%.

Black wattle supplies diverse economic benefits to society. Economically valuable products include tanning agents (extracted from the bark), timber, pulp, woodchips, charcoal, firewood and building materials (De Wit et al. 2001). Here we focus on the commercial production values only as time series on other social values are not readily available. Data on roundwood wattle sales for the years 2002 – 2019 were obtained from Forestry South Africa (Oberholzer and Godsmark 2020). The prices of black wattle timber were collected from NCT Co-operative Limited (Craig Norris, pers comm 2020). To obtain the total production values of black wattle timber, the prices of timber were multiplied by the quantity of wattle roundwood sales (See Fig. S2 in Supplementary Material). Black wattle is an important species for tannin

production in South Africa (Chan et al. 2015), but no time series on price and quantity data for tannin products in South Africa was available. The highest gross production value for black wattle, reported in 2011, amounted to \$202 million. The most recent reported gross production value for black wattle is \$175 million for 2018. As for avocados, GPV has grown over time, as have producer prices, so for the high and low scenarios the producer price for wattle bark in 2020 (Int. \$ 1,739/t) and 2030 (Int. \$ 2,491/t) were used to model the range in prices, whereas the model incorporates the change in price over time. The wattle bark prices were obtained from the Department of Agriculture, Forestry and Fisheries' Agricultural Statistics (DAFF 2020b). The GPV for wattle bark accounts for 10,9% of the GPV of all wattle products.

Natural Forests

As for the other focus areas, empirical data on the numbers of trees expected to succumb to PSHB in natural forests do not exist. However, data from ongoing surveys in natural forests in Knysna and George in the Western Cape indicate that, in the ca. 3000 km² surveyed in these two areas combined, 2195 trees were assessed for PSHB presence. Of these, 217 individuals were infested (ca. 9%) and 191 showed signs of beetle reproduction that will likely eventually lead to dieback and possible death (8.7%) (E van Rooyen, G Townsend, F Roets, unpubl data). It should be noted that these observations were made at a very early stage of the invasion and that not all individuals of a species will be equally susceptible due to genetic variability. Also, different forest types in South Africa contain different mixtures of tree species (Mucina and Rutherford 2006) that may differ in susceptibility. We therefore again decided to take a conservative approach and estimated that 5% of natural forest trees may succumb to PSHB in South Africa.

Deriving the monetary value of natural forests required an estimation of the value of ecosystem services, as the greatest losses in forests are associated with nonmarket values (Holmes et al. 2009). The values for ecosystem services provided by natural forests include provisioning services (e.g. food, water, raw materials), regulating services (e.g. air quality regulation, climate regulation), supporting services (e.g. nursery services and genetic diversity) and cultural services (e.g. esthetic information, recreation, cognitive development). The external costs of losing primary forest include carbon values and other ecosystem services associated with natural forests (Turpie et al. 2017). As conclusive local studies on natural forests were not available, international results were transferred to the South African context. To determine the per hectare monetary value of natural forest we used the results of Brenner et al. (2010) and De Groot et al. (2012, 2013), of which, estimate the above-mentioned ecosystem services, and transferred these to a South African context, using the benefit-transfer method. The values reported in these studies were adjusted following guidelines on the application of the benefit-transfer method (Saplaco and Francisco 1993); including adjustments for exchange rates, inflation, and Purchasing Power Parity (PPP) (actual calculations and discussions are included in the Supplementary Material: Benefit Transfer Method Equations).

The adjusted Total Economic Values (TEV) from each study for the South African context is listed in Table S.2 of the Supplementary Material. The highest TEV for natural forests is estimated at 2019 Int. \$ 6,642.87 per hectare and the lowest TEV at 2019 Int. \$ 2,111.23 per hectare. A mean value of 2019 Int. \$ 4,380 per hectare was used in the modelling.

Urban trees

Visual surveys undertaken in Johannesburg (Gauteng province), Knysna, George and Somerset West (all in the Western Cape province) showed that nearly all individuals of *Quercus robur* (English oak), *Acer negundo* (box elder) and other maples (*Acer* spp.) will die when infested by PSHB. Currently about half of London plane trees (*Platanus x acerifolia*) infested with PSHB in these areas are in decline and will likely die. For many other reproductive host trees planted in urban environments no data are available on the percentage of trees that will die. However, consultation with numerous academics and arborists working in urban areas in South Africa infested with PSHB suggests that 25% mortality is a conservative estimate. Unfortunately, no data are available on the species breakdown and numbers of trees planted in South African cities, which hampers more precise estimations of tree mortality. In the northern suburbs of Johannesburg, street tree composition is estimated to be 50% London plane trees (*Platanus x acerifolia*), 40% oak trees (*Quercus* spp.) and <5% maples (*Acer* spp.) (MJ Byrne pers comm). These same tree species, and numerous other taxa known to act as reproductive hosts for PSHB are commonly planted in urban environments throughout South Africa.

A similar approach for data collection as used for natural forests was adopted when determining the economic values of trees in urban environments. There are, however, two differences in the conversion process (See Supplementary Material for more detailed explanation): the unit of measurement is not value per hectare, but rather value per tree species; and the economic values are PPP adjusted to account for differences in value across different countries. For urban environments, the total economic value per tree as based on ecosystem services provided, based on studies by McPherson (2003), Soares et al. (2011), and Peper et al. (2007) are used. Economic values for *Platanus x acerifolia* (London plane), *Fraxinus velutina* (Modesto ash), and *Liquidambar forosansana* (Chinese sweetgum) were taken from data in McPherson (2003) for urban trees in Lisbon. Lastly, Peper et al. (2007) provided economic values for the London plane, Chinese sweetgum (which we used as a proxy for American sweetgum [*Liquidambar styraciflua*] - a host species of PSHB in South Africa), *Quercus palustris* (pin oak), *Q. rubra* (northern red oak), a variety of maple (*Acer* sp.) (which are averaged and used as a proxy for *Acer palmatum* (Japanese maple) which is a host species of PSHB in South Africa). Ecosystem services provided by urban trees include atmospheric carbon dioxide reduction; air quality improvement; stormwater runoff reductions, as well as aesthetic, property value, social, economic and other benefits.

Applying the benefit-transfer method (Equations in the Supplementary Material), the estimated Total Economic Value (TEV) of urban tree species are reported in Table S.3 in the Supplementary Material. 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 value is calculated at Int. \$25.07 per urban tree.

We estimate net present costs (assuming a six percent discount rate per annum, converted to a monthly effective rate as presented in Table 1) as the potential loss of production associated with the beetle-fungus interactions and external costs (loss of social value) for primary forest as well as urban forests. The physical removal cost (Int. \$656.55 per tree, 2019) is included in the private costs of the beetle colonization, since dead trees cannot be left in situ as they pose a potential risk of damage to property and vehicles. This cost was modelled for urban trees since it is a private cost to the municipality for removing the dead trees. It was deemed unnecessary to include removal costs for agricultural crops since our production value approach already included all private costs by definition.

A synthesis of the parameters used in the modelling is presented in Table 1 (full calculations are included in Table S.4 in the Supplementary Material). We estimate that there are 255 million urban trees in South Africa and that there is a 25% mortality rate over 10 years due to PSHB, giving a total of 63.75 million urban trees throughout South Africa which could be impacted by PSHB if no PSHB control measures are implemented (Table 1). The mean value of ecosystem services of an urban tree is estimated to be Int. \$25.07 (Int. \$8.22 – \$44.04) per tree. The private costs of removing a dead tree is calculated at Int. \$656.55 (Int. \$281.38 – \$3282.76) per tree and adding the loss of ecosystems services at a mean value of Int. \$25.07/tree, gives a baseline value of Int. \$ 681.2 (Range: Int. \$289.6 – \$3,326.8) per tree.

A full list of input parameters is given in Table S.5 in Supplementary Material. Costs are discounted to the year 2020 using net present value calculations. A baseline social discount rate of 6 percent is used following the calculation methodology of Van Zyl and De Wit (2013) and since the model time step is one month, this annual discount rate is converted to a discount rate compounded monthly. The time frame of the model is 10 years. The model uses expert information on the possible changes in beetle and fungus populations over time, and associated impacts on urban trees, primary forests, avocados and wattles, to estimate the social cost of PSHB infestations in South Africa.

The model

As we are concerned with the cost to society of PSHB, a typology is required since: i) the impact of the beetles varies among different tree species and also among different settings; and ii) the societal-wide costs of the affected trees also differ depending on species of tree and the setting within which it is situated. Fig. 3 provides the conceptual diagram for the BF-MLV-SD model. Beetle and fungus interactions result in tree mortality, which affects avocado trees, wattle trees, primary forests and urban trees. Agricultural crops (avocado, commercial forestry) are only assessed in terms of the loss of production values. Although commercial forestry losses could also impact on external costs, these are not included in the present model since most of these species are not native to South Africa. Only indigenous forests and urban trees are assessed in terms of the loss of ecosystem services values associated with tree mortality (external costs). In addition, urban trees are assessed in terms of the cost of removing dead trees (private costs). The total societal cost of beetle-fungus tree invasions is then the

sum of these private and external costs. These values do not include all costs, but the private costs due to loss of production and the external costs due to loss of ecosystem services are expected to be low compared to the private costs of removing dead trees in an urban context.

To model the social cost of PSHB invasion we use the Lotka-Volterra set of equations for the case of mutualism as described and motivated for in the section on modelling philosophy above. We do so first by means of a causal loop diagram (Fig. 4), followed by a stylised version of the model itself (Fig. 5). A causal loop diagram shows the feedback loops in this BF-MLV-SD model and indicates whether these interactions are reinforcing (R, in other words it leads to exponential growth or decline) or balancing (B, where the loop converges on some goal or steady state). The dynamics of the system are dependent on which loop is dominant at a particular point in time. The various loops in this model can be described as follows:

- R1: An increase in beetle births (fungus growth, R2) leads to an increase in beetle (fungus) densities, which increases beetle (fungus) populations.
- B1: An increase in beetle deaths (fungus mortality, B2) leads to decrease in beetle (fungus) populations.
- R3: An increase in beetle density increases beetle populations, which increases fungus density which increases fungus populations, which in turn increases beetle densities (mutualism).
- R4: an increase in host (avocado trees, wattle trees, primary forests and urban trees) growth increases host numbers, and host mortality reduces host numbers (B3).
- B4: Conceptually (although not actually modelled), an increase in host growth increases beetle populations, that increases fungus density and populations, which increases host mortality which reduces host numbers.

The stylised version of BF-MLV-SD model is provided by the stock-flow diagram model that depicts the relationships between the elements in the system through a series of equations. Fig. 5 provides an example of one of the stock-flow diagrams for the model showing beetle fungus interactions based on the Lotka-Volterra equations. In this figure, we use information on carrying capacity of avocados, urban trees, wattles, and primary forest to estimate the maximum number of hosts infected (assuming a 100% spread of the beetle). The ratio of initial number of trees infested to maximum number of trees infested then gives the initial number of beetles infesting trees. This information is then used in the BF-MLV-SD model by combining with data on carrying capacity (based on area of spread) and growth rates to model the potential spread of the beetle and fungus over time. Carrying capacity of the beetle and fungus assumes a 100% spread over the area occupied by the reproductive hosts included in the model ($k=1$). Growth of the beetle and fungus is calibrated to match the rate required to result in the tree dieback predicted by the team of experts (in the absence of control) for the different categories of trees used in this study. These growth rates, together with a list of equations and the values of the other constants in the BF-MLV-SD model, as well as the remainder of the stock-flow diagrams, are provided in Supplementary Material.

Results

Table 2 presents the estimated unmitigated social cost of Int. \$27.12bn associated with the potential spread of PSHB and its associated fungus in South Africa. The social cost of lost urban trees dominate the estimated unmitigated total social cost values, which are estimated at Int. \$26.95 bn. 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. \$169.96 m. Specifically, for primary forests, the social cost of PSHB infestation of primary forests is estimated at Int. \$121.62m, for wattle the cost of PSHB infestation on black wattle comprises Int. \$8.012m and for avocados, the cost of PSHB infestation on avocado production is \$40.33m.

Table 2

Estimated costs of the Polyphagous Shot Hole Borer beetle infestation in South Africa (2019 Int. \$ m).

	Baseline	Low	High
Urban trees	26 951.26	10 150.09	149 104.00
Primary forest	121.62	107.5	138.26
Wattle	8.01	7.05	9.15
Avocados	40.33	35.54	45.97
TOTAL	27 121.22	10 300,18	149 297.38
Note: Mean (Baseline), Low and high values are based on the range of prices and values given in the data section. Dynamic analysis using simulation modelling over 10 years. Net present value calculation at a discount rate of 6% per annum (Baseline. Low=4% and High=8%)			

The baseline simulation assumes that the social discount rate is 6%, and that the physical clearing cost of urban trees is Int. \$656.55 per tree. Expert opinion suggests that the cost of clearing trees in an urban context could vary between Int. \$281.38 and \$3282.76 per tree. Sensitivity analysis was therefore conducted by varying the physical clearing cost of urban trees between the minimum and maximum value per tree as well as the discount rate between 4% and 8%. In addition, the baseline estimation uses an average value for external costs of urban trees and sensitivity analysis was conducted for a broader range of values between Int. \$8.22 and Int. \$44.04 per tree.

The results of the low and high estimated values generated from these value ranges in the sensitivity analysis are also given in Table 2. As expected, the estimated total social cost associated with a loss of urban trees due to PSHB infestations vary widely between Int. \$10.15bn and Int. \$149.1bn. Primary forest social cost due to PSHB invasion is estimated to vary between Int. \$107.5m and Int. \$138.26m, wattle costs between Int. \$7.051m and Int. \$9.146 m, and avocado costs between Int. \$35.54m and Int. \$45.97m (2019 prices).

Discussion

The baseline unmitigated social cost of a possible PHSB beetle invasion in South Africa predict substantial economic losses to the economy and society. Other studies have calculated economic losses of ambrosia beetle invasions, but these have been limited to the timber industry in Canada (Orbay et al. 1994) and in the Southeastern US (Susaeta et al. 2016), or to US forestlands (Adams et al. 2020). Differences in model specifications and in selection of economic impacts make direct comparisons with our results difficult other than stating 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 PSHB 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 \$351bn (current prices) (World Bank, 2020). Using IMF (2020) 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 \$2.8trn. The unmitigated baseline social cost of \$27.12bn in the case of a PSHB invasion in South Africa would be in the order of 1% of the country's GDP, or expressed differently at around \$50 per year per person in South Africa. These numbers are incomplete estimates; they exclude broader indirect and induced economic impacts and are therefore conservative. At a national level the Medium Term Expenditure Framework budget for all environmental and natural resource management related to the Expanded Public Works Programmes (EPWP) in the country is in the order of \$240m per year or \$4 per year per person in South Africa.

Although the expected costs of a PSHB invasion on commercial black wattle and avocado is substantial in relation to the overall value of these sectors, a pertinent result of our analysis is that the loss of urban trees is by far the largest cost component on a national level. This finding emphasises the rationale for following an *ex ante* economic assessment approach to inform the prioritization of resources at the early stages of potentially high impact IAS. 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 has also been documented elsewhere (Aukema et al. 2011). McPherson et al. (2017), in one scenario, projected a 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 \$15.9bn, with the value of ecosystem services foregone over a 10-year period of \$616.6m. 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 US would amount to \$10.76bn (discounted 2009 values), a value that was updated to \$12.5bn 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 US are higher, but of the same order of magnitude as our estimates (63.75 million urban trees at a discounted social cost of \$26.7bn). The higher values in the US 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 US compared to South Africa.

Mitigating the future impact of PSHB in South Africa will be no easy task. Given how widespread PSHB is, eradication is impossible and management should therefore focus on reducing its further spread. Female beetles have limited flying range (500m to 2km), but this can be aided by wind to a spread rate of up to 20km per year (Leathers 2015; Owens et al. 2019). In Somerset West in the Western Cape, PSHB spread at least 3 km from the putative point of introduction in only three months, and in the opposite direction of the prevailing winds (F Roets pers obs). Natural spread is therefore substantial, but the long-distance spread of PSHB 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 (Shackleton 2018), presenting a probable pathway for long-distance spread (Fig. 6a – b). Recreational barbecue fires may arguably present an even more substantial long-distance dispersal danger as infested fire wood is often transported over many hundreds of kilometres and even into pristine natural environments (Fig. 6c). Similarly, the trade in infested nursery material may present a significant, although unproven, long-distance dispersal pathway for PSHB in South Africa (Fig. 6e). A first step, and likely the most economical of the mitigation factors in curbing long distance spread of PSHB, will be to restrict the free movement of infested planting material, wood and wood products.

Management options once PSHB has established in an area are fairly limited. Even though an economical option, currently no pheromones are available for mass trapping although the chemical lure querciverol may be useful for monitoring purposes (Byers et al. 2017). Current research is trying to identify natural enemies that may be useful as biological control agents against PSHB, but to date no such agent is available for release (Mendel et al. 2017). Within agriculture, an economical 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 further heavy infestations. A similar protocol will also likely yield good results in forestry plantations. For this reason it is advocated that heavily infested reproductive host trees in urban settings should be removed. These trees are seen as ‘amplifier’ trees that substantially enhance propagule pressure and thus future impacts on neighbouring trees. This approach, however, adds additional costs for the proper disposal of infested material (e.g. chipping followed by composting, incineration or solarisation (Jones and Paine 2015; Chen et al. 2020) (Fig. 6f). 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 Jones et al. 2017, Mayorquin et al. 2018, Grosman et al. 2019). These methods are currently being investigated in a South African context but are expensive, time consuming, and may have negative impacts on the environment and humans. Chemical treatment will therefore only be useful for high-value trees in urban, agricultural or forestry settings. It has also been shown that treatment is only beneficial during early stages of attack; once trees are heavily infested, chemical treatments will not be effective (Mayorquin et al. 2018).

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 policy makers, municipalities and citizens. As a consequence of urban tree invasion by the emerald ash borer for example, it has been demonstrated that municipal forestry budgets in the US 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 materially on the provision of other municipal services (Auditor-General South Africa 2019). The implication is that much of the unmitigated costs of PSHB invasion will be borne directly by citizens through direct expenditure on tree removal and by a loss of urban tree ecosystem services while dead and impacted trees are replaced by PSHB-resistant trees. Several studies have indicated that the additional costs of managing the standing stock of susceptible urban trees to prevent them being infested weighs up favourably 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 pro-active management of susceptible trees.

There are several limitations to the analysis and modelling presented in this paper. Although we believe that our collaborative interdisciplinary approach has produced a set of more robust ranges in the modelling parameters, large uncertainties remained, especially around urban tree invasion and management. Future work needs to gather empirical data on the private costs of not only removal, but also 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 a 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 on the national level, there may well be other substantial impacts. Pecan, macadamia, castor oil and litchi were not included as we are not convinced of major impacts. Blackwood (*Acacia melanoxylon*) has a potential 5 % mortality rate due to PSHB 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 PSHB has been assumed at zero; this is not correct as loss of trees on private land do 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, which would 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 modelling architecture for simulating alternative outcomes when key parameters are changed. Internal validation was done by the modeller and external validation in a series of interdisciplinary workshops involving the authors. The purpose is to build a model following an interactive process until sufficient confidence is generated in the model outputs that they may be deemed usable. A limitation of this modelling choice is that the mutualism model selected assumes

exponential increase in PSHB and *Fusarium* populations. Over our 10-years modelling 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. PSHB and *Fusarium* are likely to reach carrying capacity constraints 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 maximum 10 years.

Conclusions

Unmitigated baseline social cost of \$27.12bn in the case of a PSHB invasion in South Africa would be in the order of 1% of the country's GDP, or expressed differently around \$50 per year per person in South Africa. Although substantial economic damages is expected in the commercial forestry (notably black wattle) and the agricultural (notably avocado) sectors, almost all of these unmitigated damage costs are expected due to the loss of urban trees.

A co-ordinated strategy to deal with PSHB in South Africa will require a revision of legislation and the creation of policies pertaining to biological invasions. Currently, there is no co-ordinated management of invaders in urban ecosystems (Potgieter et al. 2020), a critical oversight as shown in this study. The governance of IAS in general, and PSHB in particular, would require re-alignment of priorities between various spheres of government and enhanced involvement of private actors. For example, given the multiple sectors affected by PSHB, cross-sectoral co-ordination will be essential on aspects such as movement, removal, disposal of infested wood and the destroying of heavily infested reproductive host trees in municipalities (Paap et al. 2020). The details on the efficacy of a governance framework to manage high-impact early stage IAS such as PSHB is recommended for further research.

Declarations

Acknowledgements

Funding for this work was provided by the DSI-NRF Centre of Excellence for Invasion Biology (NRF grant no. 41313). DMR acknowledges additional support from the Oppenheimer Memorial Trust (grant 18578/03) and the Millennium Trust. For discussions and/or comments on drafts of the paper we thank Sarah Davies, Andrew Liebhold, Christo Marais, Luke Potgieter, Guy Preston and Brian van Wilgen.

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Figures

Figure 1

Locations in South Africa where the presence of the Polyphagous Shot Hole Borer has been confirmed, by identification of the beetle based on morphology and DNA sequence, or by isolation and molecular identification of the fungal symbiont *Fusarium euwallaceae*, from wood tissue samples (current 21 December 2020). Map created using QGIS [QGIS.org (2020) QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>] Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

A Female Polyphagous Shot Hole Borer (PSHB) beetle (*Euwallacea fornicatus*, length ca. 1.8 mm, photo by S. Bush). B Galleries of PSHB in Pecan nut (*Carya illinoensis*) wood showing the black staining caused by the mutualistic fungus *Fusarium euwallaceae*. Although not considered a reproductive host, individuals were able to breed in this detached wood sample of Pecan nut likely due to prolonged disconnect from the plant defense system, demonstrating that wood of non-reproductive hosts may become suitable for beetle breeding when the host is severely stressed. C Breeding galleries of PSHB and

brown staining caused by *F. euwallaceae* in the wood of castor bean plant (*Ricinus communis*), an invasive species in South Africa. D Entry holes of PSHB in the trunk of the commercially planted forestry tree *Acacia mearnsii*. E Entry holes of PSHB and grey staining under the bark caused by *F. euwallaceae* on the indigenous reproductive host *Harpephyllum caffrum*. F Gallery system of PSHB and bright red staining in wood caused by *F. euwallaceae* on the indigenous reproductive host *Psoralea pinnata*. G Historically significant large English oak tree (*Quercus robur*) in the town of George showing leaf yellowing, leaf drop and dieback symptoms after infestation with PSHB. H Same tree, ca. two years after initial detection of PSHB and subsequent removal due to the danger posed by falling dead branches. I Signs erected on infested trees throughout the town of George informing the public of the danger posed by dead and dying trees due to the PSHB invasion.

Figure 3

Conceptual diagram for the invasion of trees by the Polyphagous Shot Hole Borer beetle in South Africa and the associated costs of the ensuing dieback

Figure 4

Causal-loop diagram showing the main feedback loops in the Beetle-Fungus Mutualistic Lotka-Volterra System Dynamics model

Figure 6

A Pile of fire wood in an informal settlement in South Africa. Fire wood is an essential resource in poorer communities throughout South Africa, however, the movement of infested fire wood presents a major pathway for the unintentional dispersal of the Polyphagous Shot Hole Borer (PSHB). The pile of wood pictured here has been placed adjacent to a known reproductive host, London plane (*Platanus x acerifolia*), which would facilitate establishment of a new PSHB outbreak/infestation, should the wood be

infested. B Pile of fire wood ready for transport to communities for essential energy production. C Camping in a near pristine natural forest park on the south coast of South Africa. The fire wood used to make the fire in the background was sourced from outside the park. Native trees at this particular camping site have been confirmed to be infested with PSHB. D Nursery stock for sale to the public that have been infested with PSHB. E. Same, close up of entry points on some plant individuals. Although not demonstrated yet, infested nursery stock may present a significant pathway for the long distance dispersal of PSHB. F. Felling and chipping of infested London plane trees in the town of Somerset West. Proper disposal of infested wood requires chipping to a minimum of ca. 5 cm followed by composting, incineration or solarization. The wood chips here are transported in a sealed truck to an incineration plant for the production of electricity. G Trunk injection to deliver therapeutic/preventative pesticide and fungicide treatments.

Supplementary Files

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